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Spatio-temporal trait change in selected insect species along land-use gradients

Raumzeitliche Merkmalveränderungen in ausgewählten Insekten-Arten entlang von Landnutzungsgradienten

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von
Silvia Keinath M. Sc.

Präsidentin der Humboldt Universität zu Berlin
Prof. Dr.-Ing. Dr. Sabine Kunst

Dekan der Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin
Prof. Dr. Dr. Christian Ulrichs

Gutachter/innen

1. PD Dr. Mark-Oliver Rödel
2. Prof. Dr. John A. Nyakatura
3. Prof. Dr. Jens Rolff
4. PD Dr. habil. Ralph Menzel

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Spatio-temporal trait change in selected insect species along land-use gradients

Abstract

During the Anthropocene increasing human induced environmental changes have led to rapid transitions from natural to novel ecosystems. Species that persist during this transition process may respond to these new conditions by altering their traits. This may enable some species to persist where others disappear due to their lack of adaptability to these new conditions.

In this thesis, I aim to understand what enable selected insect species to persist during human induced rapid environmental changes. I use morphology and biochemistry as a proxy for species' adaptations in the German Berlin-Brandenburg area, an area that is characterized by increasing urbanisation and agricultural land-use over the past 150 years. For retrospective analyses over a spatio-temporal gradient, I examined voucher specimens from natural history museums combined with newly collected specimens.

In paper 1, I examine changes in flight-to-light dependent traits in the moth species *Agrotis exclamationis* in response to increasing artificial night light in the same region over the past 137 years. For these analyses I use retrospective radiance values based on satellite data from the years 2012 to 2019. Along the spatial gradient I could not find any trait changes. However, I verified changes in body size and females' eye-size over time, although this was not directly related to artificial night light. I suggest that artificial night light influences trait changes indirectly by reinforcing habitat fragmentation and influencing females' sighting of host-plants. However, I could show a trend between smaller eyed females and increasing artificial night light over time. This provides, the first evidence that morphological trait changes in response to increasing artificial night light might already taking place.

In the second paper I investigate if increasing urbanisation and land-use for agriculture across space and time (the past 125 years) have an influence on body size and biochemistry in two ground beetle species, *Harpalus affinis* and *Harpalus rufipes*. I found no spatio-temporal changes in both species' female body size but identified a decrease in male *H. rufipes*' body size in the city, whereas their sizes stayed constant in rural areas over time. I discuss different activity pattern of both species as the reason for these findings. The biochemical examinations show that intense application of fertilizer influences the biochemistry of specimens living in agricultural habitats. This, results in stable nitrogen isotope signatures in their tissues that are mostly higher than those living in urban habitats. However, I show that some urban habitats might be equally enriched with nitrogen (as reflected in the specimens' tissues), indicating the heterogeneity of urban habitats.

In paper 3, I investigate the effects of human induced environmental changes on the frequency of colour change in the ground beetle species *Harpalus affinis* between urban and rural habitats over the past 125 years. I found sexual dichromatism, and similar colour morphs between males and females over time, with the exception of females examined from urban regions. In this case, bronze colour morphs in females were more abundant in times with high levels of soot pollution in the city, whereas green colour morphs became more dominant with decreasing levels of soot pollution over time. I interpret this finding to be driven by natural

selection of the less cryptic colour morph during the respective time period, whereas the lack of any change in colour morph frequencies in males is likely the result of sexual selection.
These studies show that rapid human induced environmental changes are triggering morphological and biochemical trait changes in species that persist in altered habitats across space and time. However, these trait changes are dependent on the species, their activity pattern and sexes. Additionally, I show that some trait changes are not clearly verifiable at present due to the relatively short timeframe in which human induced environmental changes are taking place.

Kurzfassung

Während des Anthropozäns führten zunehmende, durch Menschen verursachte Umweltveränderungen zu rasanten Übergängen von naturnahen zu neuartigen Ökosystemen. Arten die in Ökosystemen während dieser Übergänge überdauern, könnten Veränderungen ihrer Merkmale aufweisen, die sie befähigen, sich an die neuen Bedingungen anzupassen. Andere Arten hingegen verschwinden aus neuartigen Ökosystemen da sie sich nicht an die rasant entstehenden neuen Umweltbedingungen anpassen können.

In meiner Dissertation versuche ich anhand ausgewählter Insekten-Arten zu verstehen, welche Merkmale es Arten ermöglichen in Zeiten rasanter, von Menschen verursachter Umweltveränderungen zu überdauern. Hierzu untersuche ich, stellvertretend für die Fähigkeit der Adaption, morphologische und biochemische Merkmale von Arten aus der Region Berlin/Brandenburg in Deutschland. Diese Region ist durch zunehmende Urbanisierung und Landnutzung für den Ackerbau innerhalb der letzten 150 Jahre gekennzeichnet. Für rückblickende Analysen entlang eines raumzeitlichen Gradienten untersuchte ich Sammlungsexemplare aus Naturkundemuseen die durch neu gesammelte Exemplare erweitert wurden.

In Paper 1 untersuche ich in der Nachtfalterart *Agrotis exclamationis* Veränderungen von Merkmalen, die ein Verhalten begünstigen vom Licht angezogen zu werden, als Antwort auf die Zunahme künstlicher Lichtquellen in der Nacht in einer Region über die letzten 137 Jahre. Für diese Analysen verwende ich zurückwirkende Radianz-Werte basierend auf Satellitendaten der Jahre 2012 bis 2019. Entlang des räumlichen Gradienten konnte ich keine Merkmalsveränderungen nachweisen. Allerdings konnte ich Veränderungen der Körpergrößen und in Weibchen Veränderungen der Augengrößen über die Zeit nachweisen. Beide Veränderungen sind jedoch nicht direkt auf zunehmendes künstliches Licht in der Nacht zurückzuführen. Ich diskutiere den indirekten Einfluss künstlichen Lichts in der Nacht auf die nachgewiesenen Merkmalsveränderungen als Verstärkung der Habitat Fragmentierung sowie einer Beeinflussung der Sicht von Weibchen auf deren Wirtspflanzen. Allerdings konnte ich zeigen, dass in Weibchen ein Trend zwischen kleineren Augen und zunehmenden künstlichem Licht in der Nacht über die Zeit zu erkennen ist. Dies könnte auf einen ersten Hinweis hindeuten, dass morphologische Merkmalsveränderugen als Antwort auf zunehmendes künstliches Licht in der Nacht bereits stattfinden.

In Paper 2 untersuche ich ob zunehmende Urbanisierung und Landnutzung für den Ackerbau über die letzten 125 Jahre sowie zwischen beiden Landnutzungstypen einen Einfluss auf die Körpergrößen und Biochemie zweier Laufkäferarten, *Harpalus affinis* und *Harpalus rufipes*, hat. Ich konnte keine raumzeitlichen Veränderung der Körpergrößen in Weibchen beider Arten nachweisen, allerdings eine Abnahme der Körpergröße in männlichen *H. rufipes* in der Stadt über die Zeit, wohingegen deren Körpergrößen im ländlichen Raum über die gleiche Zeit konstant blieben. Ich diskutiere diese Ergebnisse als ein Resultat verschiedener Aktivitätstypen beider Arten. Die bioschemischen Untersuchungen zeigen, dass der intensivierte Einsatz von Düngemitteln einen Einfluss auf die Biochemie derer Käfer hat, die in Ackerlandschaften vorkommen. Dies zeigt sich in meist höheren Anreicherungen stabiler

Stickstoff-Isotopen in deren Geweben im Vergleich zu Käfern die im urbanen Raum leben. Allerdings konnte ich zeigen, dass einige urbane Habitate einen ähnlich hohen Stickstoffgehalt wie Ackerlandschaften aufzuweisen scheinen, was sich in den Geweben der dort lebenden Käfer wiederspiegelt und auf eine hohe Heterogenität urbaner Habitate hinweist.

In meiner 3. Publikation untersuche ich die Auswirkungen der durch Menschen verursachte Umweltveränderungen auf Farbmorph-Häufigkeiten der Laufkäferart *Harpalus affinis* zwischen urbanen und ländlichen Regionen über die letzten 125 Jahre. Ich konnte einen Sexualdichromatismus nachweisen sowie generell konstant bleibende Farbmorphen entlang der raum-zeitlichen Gradienten in Männchen und Weibchen, außer in den Weibchen die im urbanen Raum über die Zeit untersucht wurden. Hierbei war in Zeiten mit hoher städtischer Luftverschmutzung durch Ruß die bronze Farbmorphe der Weibchen in höhere Abundanz vertreten, wohingegen die grüne Farbmorphe mit abnehmender Luftverschmutzung im Laufe der Zeit an Häufigkeit zunahmen. Ich interpretiere diese Ergebnisse als ein Resultat der natürlichen Selektion der jeweils am wenigsten für Prädatoren auffälligen Farbmorphe in der entsprechenden Zeit. Das Fehlen einer Änderung der Farbmorph-Häufigkeit bei den Männchen interpretiere ich hingegen als Ergebnis der sexuellen Selektion.

In meinen Untersuchungen konnte ich zeigen, dass rasante, von Menschen verursachte Umweltveränderungen morphologische und bioschemische Merkmalsveränderungen in Arten, die in veränderten Lebensräumen überdauern, verursachen können. Allerdings sind diese Merkmalsveränderungen abhängig von der jeweiligen Art, deren Aktivitätstyp und Geschlecht. Zusätzlich konnte ich zeigen, dass manche Merkmalsveränderungen derzeit nicht klar nachweisbar sind aufgrund der relativ kurzen Zeit in der durch Menschen verursachte Umweltveränderungen stattfinden.

Preface and author's contributions

This thesis contains an introductory part and a synthesis section that summarises the most important findings from the papers. The results of this thesis are presented in three scientific papers of which one is published, one is accepted, and one is submitted. The contributions of the co-authors to each paper are described below. From all three papers, the PhD candidate (Silvia Keinath) is the first author.

The papers cover the following topics:

Paper 1

Keinath, S., Hölker, F., Müller, J., & Rödel, M.-O. (2021). *Impact of light pollution on moth morphology – a 137-year study in Germany.* Accepted on 27th of May 2021 in Basic and Applied Ecology - Urban ecosystems – their potentials, challenges and solutions. https://doi.org/10.1016/j.baae.2021.05.004

Silvia Keinath, Mark-Oliver Rödel, and Franz Hölker contributed conception and design of the study. Silvia Keinath collected field data (partly), did the measurements (entire), performed the statistical analysis (entire), prepared graphics (entire), and wrote the first draft of the manuscript (entire). All authors read, commented on, and approved the final version of the manuscript.

Paper 2

Keinath, S., Frisch, J., Müller, J., Mayer, F., Struck, U., & Rödel, M.-O. *Body sizes and dietary niche of two ground beetle species from urban and rural populations, tracked from 1900 to today.* Submitted on 23th of December, 2020.

Silvia Keinath, Mark-Oliver Rödel, Johannes Frisch, Johannes Müller, Frieder Mayer, and Ulrich Struck contributed conception and design of the study. Johannes Frisch organized the database. Ulrich Struck performed stable isotope measurements. Silvia Keinath collected field data (partly), did the measurements (entire), performed the statistical analysis (entire) and wrote the first draft of the manuscript (entire). All authors read, commented on, and contributed to the final version of the manuscript.

Paper 3

Keinath, S., Frisch, J., Müller, J., Mayer, F., & Rödel, M.-O. (2020). *Spatio-temporal color differences between urban and rural populations of a ground beetle during the last 100 years*. Frontiers in Ecology and Evolution – Urban Ecology, 7, Art. 525. https://doi.org/10.3389/fevo.2019.00525.

Silvia Keinath, and Mark-Oliver Rödel contributed conception and design of the study. Johannes Frisch organized the database. Silvia Keinath collected field data (partly), did the measurements (entire), performed statistical analysis (entire), prepared graphics (entire) and wrote the first draft of the manuscript (entire). All authors read, commented on, and approved the final version of the manuscript.

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Great thanks further go to Dirk Berger from the Naturkundemuseum Potsdam and Manfred Gerstberger from the ORION association for providing my work with museum vouchers from their collections, and to Larissa Schaub (University of Potsdam), Sascha Buchholz (TU, Berlin), and Ralph Platen (ZALF), that kindly supported me with insect samples from their fieldworks.

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Contents

1 Introduction

1.1 The Anthropocene

We live on a highly dynamic planet which is constantly changing in response to natural processes over time (Steffen et al., 2004). These continuous changes lead to evolutionary processes in species resulting from adaptations to changing conditions (Darwin, 1875; Waddington, 1959).

The spread of humans across the planet, has led to an acceleration of this originally long-term change of environments due to rapid land-use for human living space (CRGEC, 1991) and agriculture (Tilman et al., 2001). Humans altered their environments in a dimension similar to that of significant geological forces, justifying the assignment of this geological epoch as the 'Anthropocene' (Steffen et al., 2011). There is no specific date for the beginning of this epoch, but it is suggested that the latter part of the 18th century marked the starting point. At this time, the industrial revolution spread from England to countries in Europe and North America, making global effects of human impacts clearly visible during the past two centuries (Steffen et al., 2011).

The human world population comprises 7.7 billion people, with a projected increase to 9.7 billion people by 2050 (United Nations, 2019). Currently 75 % of the ice-free land of our planet is human influenced (Ellis et al., 2010) to varying degrees of intensity (Liu et al., 2002). Between 1982 and 2016 Song et al. (2018) identified that of all land changes, 60 % are associated with direct human land-use and 40 % are indirectly affected (potentially via climate change).

1.2 Agricultural land-use and urbanisation

With a steady increasing human population, the demand for food and fuel increases (Foley et al., 2011). Due to the agricultural revolution in the second half of the 20th century agricultural productivity in Europe and North America was intensified by economic and technological incentives (Blaxter and Robertson, 1995; Gardner, 1996; Erisman et al., 2008), resulting in steadily increasing amounts of intensely managed agricultural land globally (Foley et al., 2011). By the year 2000, agricultural land occupied roughly 38 % of the Earth's terrestrial surface (Ramankutty et al., 2008). The large amount of land utilized for extensive monoculture cultivations results in environmental eutrophication due to intense application of biological and chemical fertilizer (Smith, 2003; Bouwman et al., 2009). Agricultural land-use also leads to the loss of habitat heterogeneity (Benton et al., 2003), which has resulted in widespread declines in farmland biodiversity across taxa in recent years (Fuller et al., 1995; Flowerdew, 1997; Sotherton and Self, 2000).

In addition, the number and size of urban settlements is increasing rapidly and the percentage of people living in urban areas is growing (Soundranayagam et al., 2011). While in 1950 30 % of the world's population lived in cities, it is projected that 68 % of the world's population will be living in cities by 2050 (United Nations, 2019). Urbanisation leads to drastic environmental changes such as air pollution, resulting from high traffic density and exhausted industrial gases (Fenger, 1999; Baklanov et al., 2015), light pollution due to artificial night lighting (Sutton, 2003; Kyba et al., 2017b), as well as loss and fragmentation of the environment due to building and infrastructure construction (Liu et al., 2016). Cities additionally exhibit higher temperatures than their rural surroundings, due to sealing, high buildings and low vegetation cover (Oke, 1973) (Fig. 1). These factors have multifaceted negative and positive effects on species living in cities (McKinney, 2008). Urbanisation removes habitats for many native species (McKinney, 2006), leading to a decline in some taxa (Davis, 1978; Germaine and Wakeling, 2001; Kim and Pauleit, 2005). Some taxa however, exhibit population increase (Frankie and Ehler, 1978; Kühn et al., 2004; McKinney, 2006), due to the higher habitat heterogeneity in urban areas compared to rural areas over small spatial scales (Kühn et al., 2004).

1.3 Effects of ecological novelty on communities and species

Land-use for agriculture and urbanisation are examples of human induced changes leading to rapid transitions from historically natural to human influenced environments over time (Fig. 1). These developments are transforming the abiotic and biotic conditions on Earth (Turner and Clark, 1990; Steffen et al., 2004; Millennium Ecosystem Assessment, 2005), defined as ecological novelty (Kueffer, 2015).

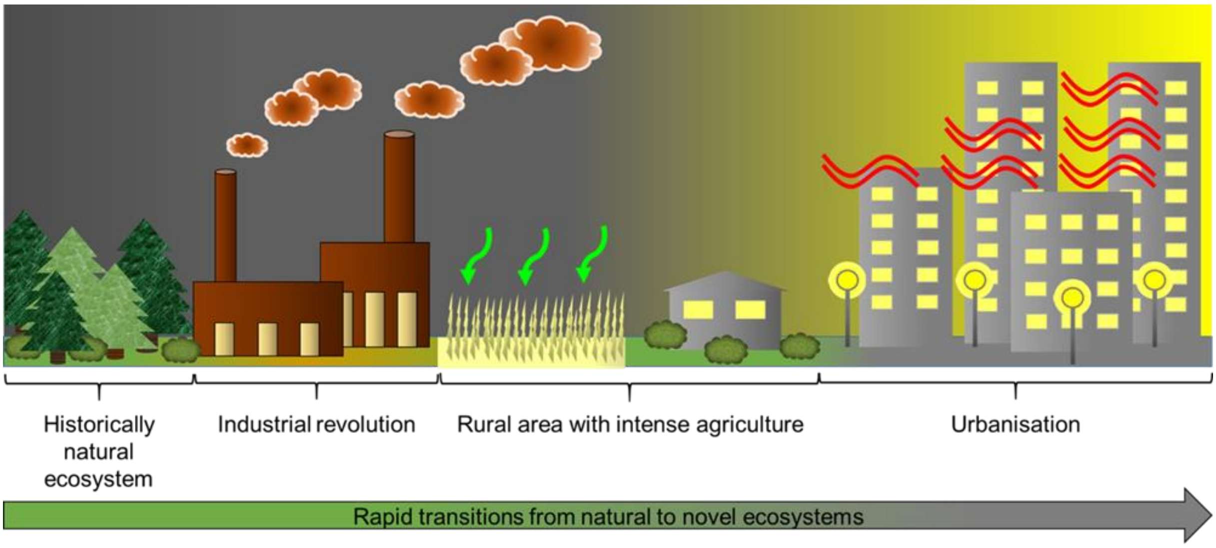

Figure 1 Rapid transitions from historically natural to novel ecosystems marked by land-use for industry, agriculture and urban space, including the following anthropogenic impacts on the environment: Soot pollution from industry (brown clouds), application of fertilizer in agricultural landscapes (green arrows), artificial night light in urban areas (yellow light sources), and urban heat (red waves). Rapid transitions in space are also reflected over time (arrow below).

Ecological novelty is clearly defined as man-made (Vitousek et al., 1997; Turner and Clark, 1990), and is characterised by the large magnitude and rapid rates of current environmental changes (Vitousek et al., 1997; Steffen et al., 2004; Fischlin et al., 2007; Millennium Ecosystem Assessmant, 2005). It is also characterized by its multi-dimensional changes, including multiple co-occurring factors (Kueffer et al., 2013). This makes ecological novelty highly variable, unknown and unpredictable on a global scale (Kueffer, 2015) with unknown triggers and consequences for therein living species (Hobbs et al., 2013; Jeltsch et al., 2013).

Ecological novelty is shaping novel ecosystems that differ in their functions and species compositions from those that preceded human impacts (Hobbs et al., 2013). These novel communities are composed of species that have never interacted in their evolutionary past (Tockner et al., 2011, Lurgi et al., 2012). Some species recently invaded into such systems (Kenis et al., 2009; Oduor et al., 2016), whereas others disappeared due to an inability to adapt in the face of new conditions (Maas et al., 2002; Brunk and Wiegleb, 2006; Kenis et al., 2009; Ziegler, 2011). However, there are still species that persist throughout rapid transitions from natural to novel ecosystems (van´t Hof et al., 2011; Doudna and Danielson, 2015; Niemeier et al., 2020). Unfortunately, it is unclear what the general conditions are under which trait changes are promoted/prevented, that subsequently determine a species adaptability to changing environments (Palkovacs et al., 2011).

1.4 Importance of museum vouchers

Transitions from natural to novel ecosystems take place over relatively short timeframes in comparison to most natural evolutionary processes (Vitousek et al., 1997; Steffen et al., 2004; Fischlin et al., 2007; Millennium Ecosystem Assessment, 2005). However, these timeframes are still too long to make changes in physiology and behaviour in species that persist through times of human-induced environmental alterations directly verifiable. But there is a possibility to study species over longer periods by examining preserved specimens of natural history museum collections (Rocha et al., 2014). Morphological traits of museum voucher specimens can be used as a proxy for species' ecological and physiological adaptations across time (Doudna and Danielson, 2015; Niemeier et al., 2020). By comparing current samples with museum specimens from the same areas, it is possible to obtain data across environmental transitions over a spatio-temporal gradient (van't Hof et al., 2011; Doudna and Danielson, 2015; Niemeier et al., 2020).

1.5 Insects as study species

Insects are well presented in collections of natural history museums, comprising many species which persisted though times of human induced environmental change. About 54 % of the more than one million extant described animal species are insects, distributed over a wide geographical area (Schowalter, 2000; Chapman, 2006). Their sensitivity to environmental changes can provide an early warning for alterations, and allow for continuous assessment over a wide range of stresses. Insects also respond quickly to environmental changes due to their short generation times, and high reproductive capacity (Peck et al., 1998; Stange and

Ayres, 2010). As such, insects serve as excellent biological indicators (Noss, 1990; Peck et al., 1998), and have been used to determine human-driven changes in the environment, such as pollution, habitat loss, habitat fragmentation (McGeoch, 1998), and climate change (Bale et al., 2002). The latter is affecting insects at a high rate because climate has a strong direct influence on their development, reproduction, and survival (Bale et al., 2002).

For my thesis I chose three insect species that are verifiable due to well-presented vouchers in collections of the Museum für Naturkunde, Berlin and the Naturkundemuseum Potsdam. These species persisted across times of human induced environmental changes and occur in habitats with different degrees of human impacts in my study area, the German Berlin-Brandenburg area.

The moth (Lepidoptera, Noctuidae) species *Agrotis exclamationis* (Linnaeus, 1758) is widespread in the Palaearctic. This species exhibits forewings with lengths of 15 to 19 millimetres, and colours ranging from pale to dark brown, marked by dark stigmata (Ebert et al., 1997). It is a nocturnal pollinator that occurs in glades, grasslands, parks, gardens, on ruderal sites and forest edges, but rarely at clearings (Ebert et al., 1997) (Fig. 2).

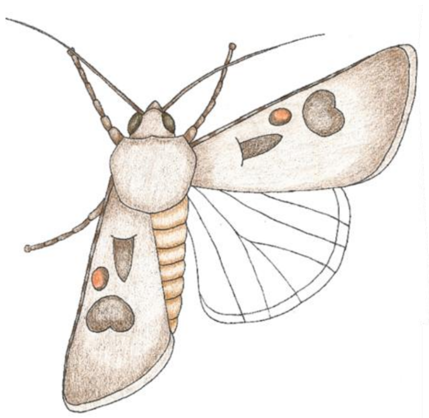

Figure 2: Drawing of the moth species *Agrotis exclamationis*. Drawn by Silvia Keinath.

The ground beetle (Coleoptera, Carabidae) species *Harpalus affinis* (Schrank, 1781) is widespread in the Palaearctic and exhibits variable metallic coloration (Wrase, 2004). The species is medium-sized (8.5-12 mm), diurnal and predominantly feeds on weed seeds as well as occasionally on insect larvae (Townsend, 1992; Sunderland et al., 1995). Adults are winged and volant and breed in the spring (Townsend, 1992; Trautner, 2017) (Fig. 3).

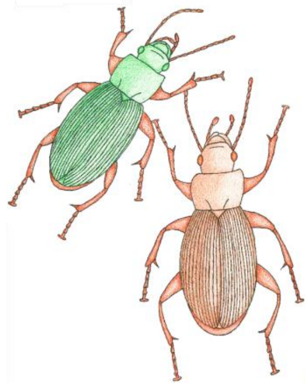

Figure 3 Drawings of a bronze and green colour morph of the ground beetle species *Harpalus affinis*. Drawn by Silvia Keinath.

Harpalus rufipes (De Geer, 1774) is another ground beetle species (Coleoptera, Carabidae), that is widespread in the Palaearctic and black in colour with brown/red legs (Wrase, 2004). The species is medium-sized (11-16 mm) and nocturnal (Wrase, 2004). Adults breed in summer and are winged and volant (Trautner, 2017). They predominantly feed on weed seeds but also on insect larvae (Bažok et al., 2007; Trautner, 2017) (Fig. 4).

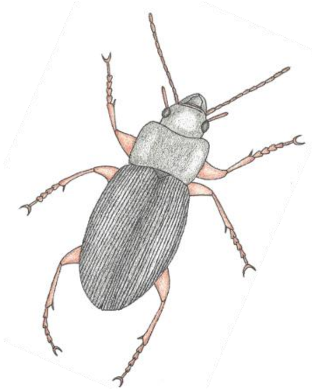

Figure 4 Drawing of the ground beetle species *Harpalus rufipes*. Drawn by Silvia Keinath.

Both ground beetle species occur across a wide range of different habitats, including less human impacted, near natural open landscapes (Townsend, 1992; Holec et al., 2006), semi-natural landscapes (Anjum-Zubair et al., 2015), vineyards, grasslands (Trautner, 2017), arable fields (Sunderland et al., 1995; Harrison and Gallandt, 2012), and in urban green spaces (Deichsel, 2006).

1.6 Interest of this work

The aim of my thesis is to understand what enables insect species to persist over a spatio-temporal gradient of human induced transitions from natural to novel ecosystems in the Berlin-Brandenburg area, Germany. By using morphological and biochemical traits of museum vouchers and recently collected specimens of these three insect species, I purpose to examine adaptations to human induced environmental conditions.

2 Synthesis

2.1 The Berlin-Brandenburg area, Germany

For my thesis all the papers examine morphological and biochemical trait changes in the chosen insect species over a 137 (paper 1) and 125-year period (paper 2 and 3) in the German Berlin-Brandenburg region. This region consists of the fast-growing metropolis of Berlin, whose expansion and population increase started toward the end of the 19th century. The high level of urbanisation (Antrop, 2000; Kratke, 2000) supports a current population (in 2020) of nearly 3.8 million inhabitants (Amt für Statistik Berlin-Brandenburg, 2021). The federal state of Brandenburg, surrounding Berlin, mostly consists of rural landscapes, ranging from less human induced, near natural to intensively managed agricultural monocultures (Cochrane and Jonas, 1999) (Fig. 5).

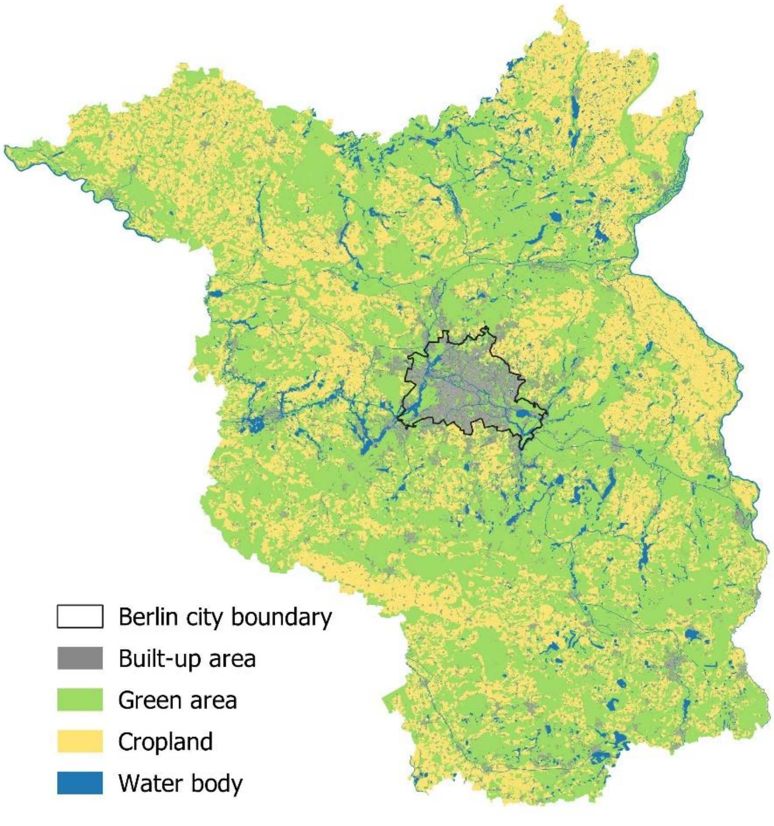

Figure 5 Land-use map of the Berlin-Brandenburg area, Germany between the years 2009 and 2015. The rural federal state of Brandenburg, mostly consisting of agricultural and near-natural landscapes, is surrounding the metropolis of Berlin (Landesamt für Umwelt, 2009; Senate Department for Urban Development and Housing, 2014; Maps merged and prepared by Anne Hiller).

2.2 Flight-to-light associated traits

Increasing artificial illumination during night affects moth's activity (van Langevelde et al., 2011; Owens et al., 2020) and is an increasing factor in the city of Berlin (Kyba et al., 2017a). Moths use celestial light sources for orientation (Baker and Sadovy, 1978), and are distracted by artificial light sources where they are captured in the light beam and become easy prey for predators or die due to exhaustion (Eisenbeis, 2006; Degen et al., 2016). Thus, I expect in paper 1, adaptations in morphological traits that reduce flight-to-light behaviour over time in the moth species *Agrotis exclamationis* to artificial night light. Body size and forewing lengths are traits indicating flight- and dispersal abilities as larger, longer winged specimens show better flight- and dispersal abilities (Beall and Williams, 1945; Nieminen et al., 1999; Slade et al., 2013). Eye size indicates sensitivity to light as specimens with larger eyes are shown to be more sensitive to light (Rutowski et al., 2009). Thus, I estimate in paper 1, a decrease in these traits due to decreased mobility and sensitive vision as a response to increasing artificial night light over space and time. To determine levels of light pollution over the past 137 years, I use back-calculated radiance values based on recent satellite data of the Berlin-Brandenburg region. I could show that body sizes in both sexes increased and eye-size decreased only in females over time. However, these results were not directly associated with increasing artificial night light. In the discussion I explain that increasing habitat fragmentation might be a driver for increasing body size (Merckx et al., 2018), and changes in host plant composition due to urbanisation (Sukopp and Werner, 1983; Zerbe et al., 2002) as a driver for decreasing eye-size in females. Females are dependent on their eye-size when choosing host plants for oviposition (Bernays, 2001), whereas males are dependent on their eye-size for mating (Grant, 1987). Based therein I discuss the lack of changes in males' eye-size. I further discuss that increasing artificial night light might indirectly influence both morphological trait changes, as it was shown to reinforce fragmentation of nocturnal habitats (Degen et al., 2016), and influence female moths' vision when searching for host plants (Callahan, 1957). Moreover, I found a trend of smaller eyed females associated with increasing artificial night light over time (Fig. 6). I discuss this finding as a preliminary indicator, that morphological trait change in response to artificial night light are already taking place, but that the timeframe of 137 years might be too short.

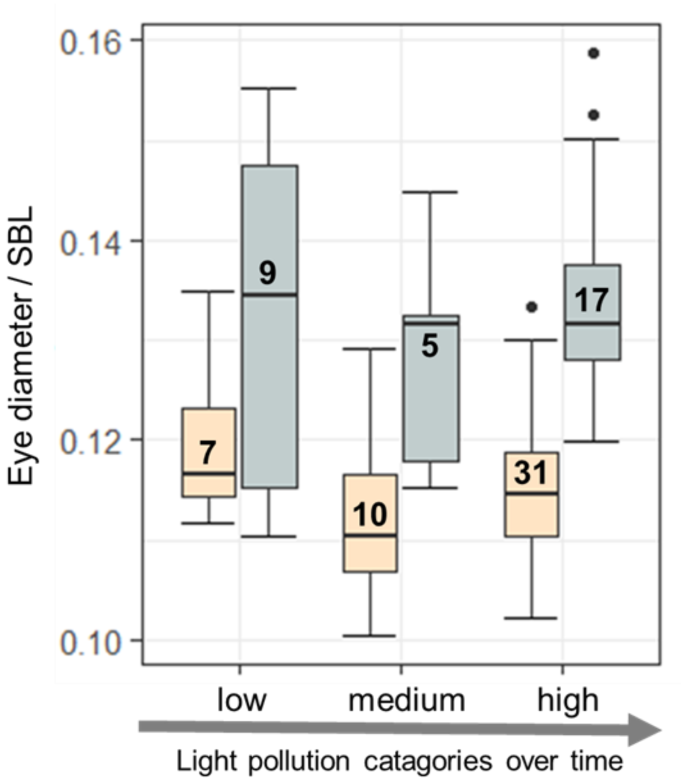

Figure 6 Mean eye diameter of right and left eyes in relation to standardized body size (eye diameter / SBL) over time (arrow) with different light pollution categories (low, medium, high) of females (reddish boxplots) and males (blue boxplots). Females show a trend for smaller eyes in areas with 'medium' and 'high' in comparison to areas with 'low' light pollution categories (p = 0.055) and a trend in the interaction between light pollution categories and years (p = 0.051). Numbers within boxplots give sample sizes. Figure taken from paper 1, figure 4.

2.3 Body size

Body size is an indicator for habitat quality (Weller and Ganzhorn, 2003; Sukhodolskaya, 2013) because ectotherm development is dependent on environmental temperatures (Atkinson, 1994; Kingsolver and Huey, 2008). Temperatures are higher in the city than in rural areas (Oke, 1973) and are increasing with increasing urbanisation (Tseng et al., 2018). Thus, in paper 2 I expect body sizes in two ground beetle species *Harpalus affinis* and *Harpalus rufipes* to be smaller now than in the past when living in the city. I verify this expectation only in *H. rufipes*' males, not in females (Fig. 7) and not in either sex of *H. affinis*. Thus, I show that different activity patterns of species might play a role when adapting to urbanisation. *Harpalus rufipes* in contrary to *H. affinis* is nocturnal (Wrase, 2004), and attracted to artificial light sources (Kegel, 1990; Szentkirályi et al., 2003) its application increased over the past 150 years in Berlin due to increasing urbanisation (Eisenbeis and Hänel, 2009; Kyba et al., 2017a). Larger males with better flight abilities might be attracted to artificial light sources resulting in an adaptive advantage of smaller males in the city over time. Body size in females may remain constant due to their generally lower mating effort (Thornhill and Alcock, 1983). As rural areas are less artificially illuminated (Rich and Longcore, 2006), body size in *H. rufipes* stayed constant over the same timeframe. *Harpalus affinis* might not be affected by artificial light at night due to its diurnal activity, explaining the lack in changes in their body sizes. Diurnal species are more dependent on their colouration than nocturnal ones. In paper 3, I show a sex specific adaptation to urbanisation across the same timeframe in colouration in this species.

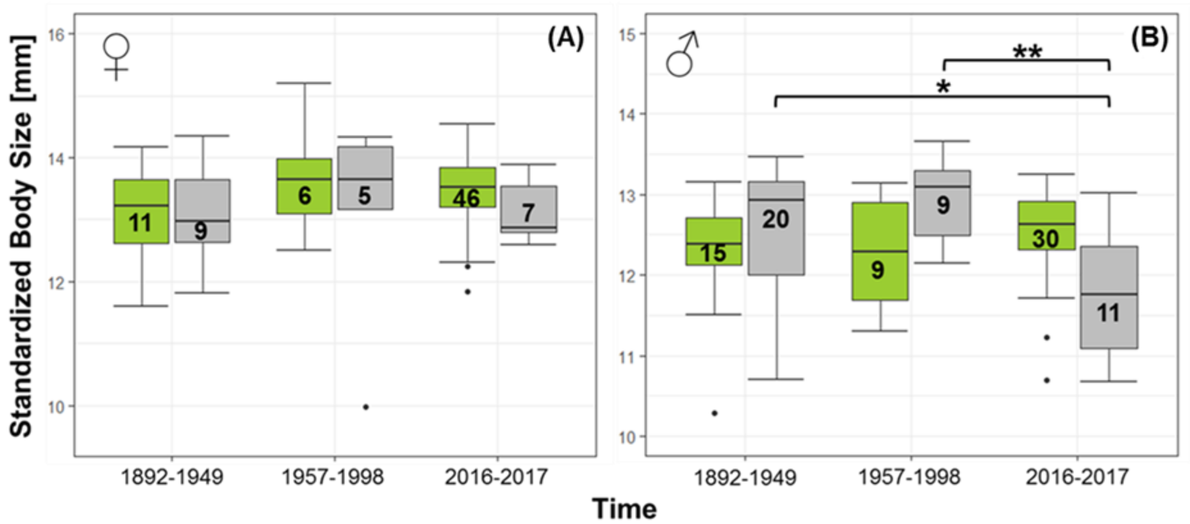

Figure 7 Body sizes of *Harpalus rufipes* females (A) and males (B) in rural (green boxes) and city (grey boxes) areas over time. Numbers within boxes indicate sample sizes, dotted brackets with stars indicate significant differences in variability of body size, brackets with stars indicate significant differences in body size (* = $p < 0.05$; ** = $p < 0.01$). Figure taken from paper 2, modified from figure 3.

2.4 Colouration

Adaptation in species' colouration due to human induced environmental changes over relatively short timeframes was already identified in the Peppered Moth *Biston betularia* in response to the industrial revolution in England (so called industrial melanism). The selective pressure that acts upon species in this case is natural selection for individuals that are less conspicuous to predators (Bishop, 1972). In paper 3, I demonstrate sexual dichromatism and sex dependent changes in colour morph frequencies in the ground beetle species *Harpalus affinis* over the past 125 years in Berlin, whereas colour morph frequencies in both sexes remained constant across the same timeframe in the rural region of Brandenburg. Females from Berlin previously exhibited bronze as the most dominant colour morph, with bronze colour morph frequency decreasing over time, along with a complementary increase in green colour morph dominance similar to that of males (Fig. 8). In times in which bronze was the dominant colour morph in females, Berlin was heavily soot polluted as a result of industrialisation (Wey, 1982) and its urban space was rapidly expanded (Buesch and Haus, 1987). These effects on the urban environment, led to natural selection for the bronze morph, which was the less conspicuous colour morph to predators (Thiele, 1977; Endler, 1988). With the establishment of environmental protection measures (UNEP/WHO, 1993; UBA, 1998;

SenStadtWohn, 2018; Pamme, 2003) and thereof decreasing levels of air pollution over time, green colour morphs in females became more dominant. In the discussion section of paper 3, I theorize that green females were likely the dominant colour morph in Berlin in pre-industrial times. The lack of changes in male colour morphs during soot polluted times may be due to sexual selection of females, resulting in a trade-off between mating male success and survival.

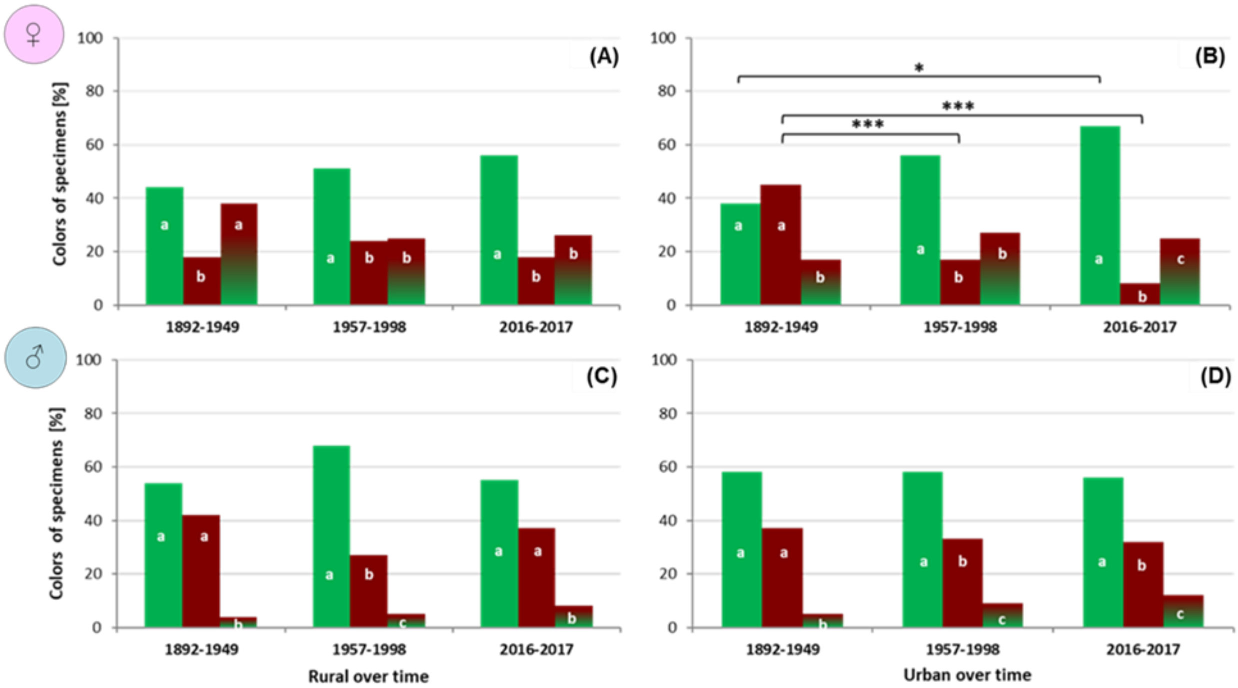

Figure 8 Percentage of *Harpalus affinis*' females (A, B) and males (C, D) colour morphs in rural (A, C) and urban (B, D) areas over time. Different letters indicate significant differences in frequencies of the three colour morphs; brackets with stars indicate significant difference between time periods (*p < 0.05; ***p < 0.01). Figure taken from paper 3, modified from figure 4 and 5.

2.5 Nitrogen enrichments

Stable isotope compositions, reflect the living conditions of an individual (Peterson and Fry, 1987). In its tissues, nitrogen is enriched into two stable isotopes $^{15}N/^{14}N$ (Rosing et al., 1998) which provide information on its trophic position (Birkhofer et al., 2011) or its respective environment. For example, species inhabiting managed agricultural landscapes show high nitrogen enrichments due to the application of fertilizer (DeNiro and Epstein, 1980; Jenkinson, 2001). In paper 2 I verify spatial differences in stable nitrogen composition in two ground beetle species *Harpalus affinis* and *Harpalus rufipes* occurring in urban and agricultural habitats. In nearly all tissues of both species, stable nitrogen signatures were higher in agricultural landscapes than city habitats (Fig. 9). However, I demonstrate that some (highly human impacted) urban habitats are equally enriched with nitrogen as intensively managed agricultural areas (Muchovej and Rechcigl, 1994; Zhu et al., 2004). I show that higher environmental nitrogen enrichments have an influence on biochemistry on both species.

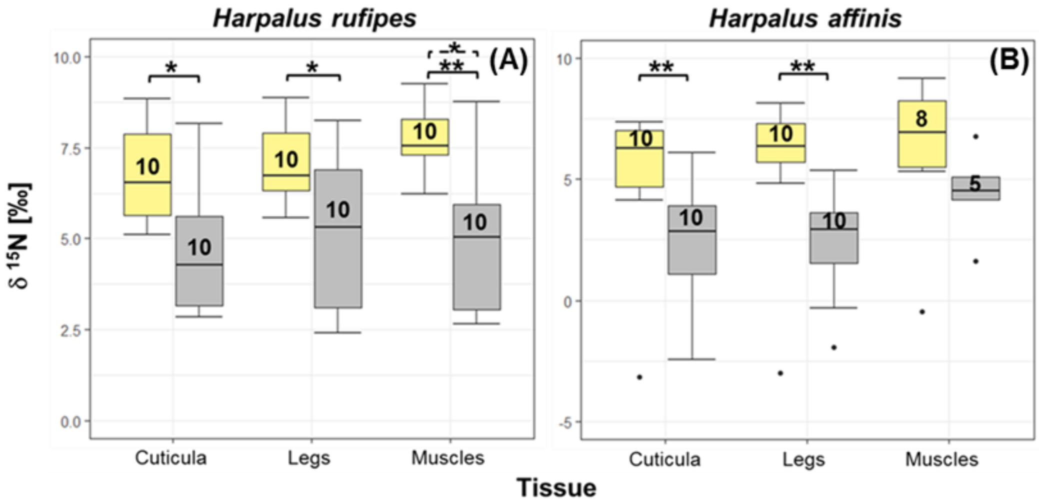

Figure 9 Stable δ ^{15}N (in ‰) in cuticula, legs, and muscles of *Harpalus rufipes* (A) and *H. affinis* (B) from agricultural (yellow boxes) and urban (grey boxes) habitats, numbers within box plots provide sample sizes, black brackets with stars indicate significant difference between stable isotope values in tissues between habitats, dotted bracket with stars indicate significant differences in variability of stable isotope values in tissues between habitats (* = $p < 0.05$; ** = $p < 0.01$). Figure taken from paper 2, modified from Figure 4.

3. Conclusions and outlook

In my thesis I identified intraspecific trait differences between different habitats with varying degrees of human impact. This was particularly apparent in the nitrogen signatures of specimens occurring in landscapes used for agriculture (due to intense application of fertilizer), compared to non-agricultural environments, as described for other Arthropods (Birkhofer et al., 2011) and amphibians (Niemeier et al., 2020). However, high nitrogen enrichments, reflected in specimens' tissues, were not exclusive to intensive agriculture habitats. Highly heterogeneous urban areas also contained habitats with equally high nitrogen enrichments, dependent on the degree of anthropogenic use, as described by Pyšek (1995) and was found to be reflected in amphibians (Niemeier et al., 2020).

I also demonstrate that morphological trait changes in insects occur across a relatively short timeframe (less than 150 years) of human induced environmental change from natural to novel ecosystems, as was already shown in moths (van't Hof et al., 2011), amphibians (Niemeier et al., 2020) and mammals (Doudna and Danielson, 2015). In particular I show that different factors affect species occurring in human induced environments. These factors, influence natural and sexual selection, resulting in morphological trait changes over time that are dependent on the respective species, their activity pattern and sexes.

However, some morphological trait changes are not clearly definable as most evolutionary processes are dependent on longer times. As some human induced environmental shifts began fairly recently, these timeframes may be too short for adaptations to visibly arise. This may be the case for the application of artificial night lights which have continuously increased in intensity since 1950s (Eisenbeis and Hänel, 2009).

To gain more insights into species' adaptations to human induced environmental changes over rapidly transitioning natural to novel ecosystems, changes in morphological traits obtained from museum vouchers could be examined over longer timeframes. However, to do so it is important to expand museum collections by including samples of recent and ongoing years. Besides increasing our knowledge of species adaptability to novel ecosystems, management of sufficient habitats and reduction of human induced stressors are important measures to assure species conservation.

4. Bibliography

Amt für Statistik Berlin-Brandenburg. *Berlins Einwohnerzahl stagniert 2020*. Available at: https://www.statistik-berlin-brandenburg.de/pms/2021/21-02-10.pdf. Last accessed 27 February 2021. 2021.

Anjum-Zubair, M., Entling, M. H., Bruckner, A., Drapela, T., and Thomas, F. 2015. Differences of spring carabid beetle assemblages between semi-natural and adjoining winter wheat. *Agricultural and Forest Entomology*, 17(4): 355-365. https://doi.org/10.1111/afe.12115.

Antrop, M. 2000. Changing patterns in the urbanized countryside of Western Europe. *Landscape Ecology*, 15: 257-270. https://doi.org/10.1023/A:1008151109252.

Atkinson, D. 1994. Temperature and organism size – A biological law for ectotherms? *Advances in Ecological Research*, 25: 1-58.

Baker, R. R., and Sadovy, Y. 1978. The distance and nature of light-trap response of moths. *Nature*, 276: 818-821. https://doi.org/10.1038/276818a0.

Baklanov, A., Molina, L. T., and Gauss, M. 2015. Megacities, air quality and climate. *Atmospheric Environment*, 126: 235-249. https://doi.org/10.1016/j.atmosenv.2015.11.059.

Bale, J. S., Masters J. M., Hodkinson, D. I., Awmack, C., Bezemer, M. T., Brown, K. V., Butterfield, J., Buse, A., Coulson, C. J., Farrar, J., Good, G. E. J., Harrington, R., Hartley, S., Jones, H. T., Lindroth, L. R., Press, C. M., Symrnioudis, I., Watt, D. A., and Whittaker, B. J. 2002. Herbivory in global climate change research: direct effect of rising temperature on insect herbivores. *Global Change Biology* 8(1): 1-16. https://doi.org/10.1046/j.1365-2486.2002.00451.x.

Bažok, R., Kos, T., Igrc Barčić, J., Kolal, V., Lazarević, B., and Čatić, A. 2007. Abundance and distribution of the ground beetle *Pterostichus melanarius* (Illiger, 1798) and *Pseudoophonus rufipes* (De Geer, 1774) in corn fields in Croatia. *Entomologia Croatica*, 11(1-2): 39-51. https://hrcak.srce.hr/39510.

Beall, G., and Williams, C. B. 1945. Geographic variation in the wing length of *Danaus plexippus* (Lep. Rhopalocera). *Proceedings of the Royal Entomological Society of London*, 20: 65-76. https://doi.org/10.1111/j.1365-3032.1945.tb01068.x.

Benton, T. G., Vickery, J. A., and Wilson, J. D. 2003. Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18(4): 182-188. https://doi.org/10.1016/S0169-5347(03)00011-9.

Bernays, E. A. 2001. Neural limitations in phytophagous insects: Implications for diet breadt and evolution of host affiliation. *Annual Reviews of Entomology*, 46: 703-727. https://doi.org/10.1146/annurev.ento.46.1.703.

Birkhofer, K., Fließbach, A., Wise, H. D., and Scheu, S. 2011. Arthropod food webs in organic and conventional wheat farming systems of an agricultural long term experiment: A stable isotope approach. *Agricultural and Forest Entomology*, 13(2): 197-204. https://doi.org/10.1111/j.1461-9563.2010.00511.x.

Bishop, J. A. 1972. An experimental study of the cline of industrial melanism in *Biston betularia* (L.) (Lepidoptera) between urban Liverpool and rural North wales. *Journal of Animal Ecology*, 41(1): 209-243. https://doi.org/10.2307/3513.

Blaxter, K., and Robertson, N. *From Dearth to Plenty: The Second Agricultural Revolution*, Cambridge University Press, Cambridge, 1995.

Bouwman, F. A., Beusen W. H. A., and Billen, G. 2009. Human alteration of the global nitrogen and phosphorus soil balances for the period 1970–2050. *Global Biogeochemical Cycles*, 23(4): 1-16. https://doi.org/10.1029/2009GB003576.

Brunk, I., and Wiegleb, G. 2006. Laufkäfer gestörter Landschaften der Niederlausitz-Bergbaufolgelandschaften. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomology*, 15: 379-382.

Buesch, O., and Haus, W. *Berlin als Hauptstadt der Weimarer Republik 1919-1933*. Walter de Gruyter & Co, Berlin, 1987.

Callahan, S. P. 1957. Oviposition response of the imago of the Corn Earworm *Heliothis zea* (Boddie), to various wave lengths of light. *Annals of the Entomological Society of America*, 50(5): 444-452. https://doi.org/10.1093/aesa/50.5.444.

Chapman, A. D. *Numbers of Living Species in Australia and the World*. Australian Biological Resources Study, Canberra, 2006.

Cochrane, A., and Jonas, A. 1999. Reimagining Berlin: World city, national capital or ordinary place? *European Urban and Regional Studies*, 6(2): 145-164. https://doi.org/10.1177/096977649900600204.

CRGEC (Committee for Research on Global Environmental Change). *Report on the working group on land use change*. Social Science Research Council, Washington, 1991.

Davis, B. N. K. Urbanisation and the diversity of insects. In Mound, L. A., and Waloff, N., editors, *Diversity of insect fauna*, pages 126-138. Blackwell, Oxford, 1978.

Darwin, C. *The Origin of Species by means of Natural Selection*. John Murray, London, 1875.

Degen, T., Mitesser, O., Perkin, K. E., Weiß, N.-S., Oehlert, M., Matting, E., and Hölker F. 2016. Street lighting: Sex-independent impacts on moth movement. *Journal of Animal Ecology*, 85(5): 1352-1360. https://doi.org/10.1111/1365-2656.12540.

Deichsel, R. 2006. Species change in an urban setting - ground and rove beetles (Coleoptera: Carabidae and Staphylinidae) in Berlin. *Urban Ecosystems*, 9: 161-178. https://doi.org/10.1007/s11252006-8588-3.

DeNiro, M. J., and Epstein, S. 1980. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, 45(3): 341-351. https://doi.org/10.1016/0016-7037(81)90244-1.

Doudna, J. W., and Danielson, B. J. 2015. Rapid morphological change in the masticatory structures of an important ecosystem service provider. *PLoS ONE,* 10: e0127218. https://doi.org/10.1371/journal.pone.0127218.

Ebert, G., Rennwald, E. and Bartsch, D. *Die Schmetterlinge Baden- Württembergs*. Band 5 - Nachtfalter III. Ulmer, Stuttgart, 1997.

Eisenbeis, G. Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. In Rich, C., and Longcore, T., editors, *Ecological Consequences of Artificial Night Lighting*, pages 281-304. Island Press, Washington, 2006.

Eisenbeis, G., and Hänel, A. Light pollution and the impact of artificial night lighting on insects. In McDonnell, M. J., Hahs, A. H., and Breuste, H. J., editors, *Ecology of Cities and Towns*, pages 243-263. Cambridge University Press, Cambridge, 2009.

Ellis, E. C., Goldewijk, K. K., Siebert, S., Lightman, D., and Ramankutty, N. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, 19(5): 589-606. https://doi.org/10.1111/j.1466-8238.2010.00540.x.

Endler, J. A. 1988. Frequency-dependent predation, crypsis and aposematic coloration. *Philosophical Transactions of the Royal Society B.*, 319(1196): 505-523. https://doi.org/10.1098/rstb.1988.0062.

Erisman, J. W., Sutton, A. M., Galloway, J., Klimont, Z., and Winiwarter, W. 2008. How a century of ammonia synthesis changed the world. *Nature Geoscience*, 1: 636-639. https://doi.org/10.1038/ngeo325.

Fenger, J. 1999. Urban air quality. *Atmospheric Environment*, 33(29): 4877-4900. https://doi.org/10.1016/S1352-2310(99)00290-3.

Fischlin, A., Midgley, F. G., Price, T. J., Leemans, R., Gopal, B., Turley, C., Rounsevell, A. D. M., Dube, P. O., Tarazona, J., and Velichko, A. A. Ecosystems, their properties, goods, and services. In Parry, L. M., Canziani, F. O., Palutikof, P. J., van der Linden, J. P. and Hanson, E. C., editors, *Climate Change 2007: Impacts, Adaptation and Vulnerability*, pages 211-272. Cambridge University Press, Cambridge, 2007.

Flowerdew, R. J. Mammal biodiversity in agricultural habitats. In Kirkwood, C. R., editor, *Biodiversity and Conservation in Agriculture*, pages 25-40. British Crop Protection, Council, 1997.

Foley, J. A, Ramankutty, N., Brauman, K. A, Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., and Zaks, D. P. M. 2011. Solutions for a cultivated planet. *Nature* 478: 337-42. https://doi.org/10.1038/nature10452.

Frankie, G. W., and Ehler, L. E. 1978. Ecology of insects in urban environments. *Annual Review of Entomology*, 23: 367-387. https://doi.org/10.1146/annurev.en.23.010178.002055.

Fuller, J. R., Gregory, D. R., Gibbons, W. D., Marchant, H. J., Wilson, D. J., Baillie, R. S., and Carter, N. 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, 9(6): 1425-1441. https://doi.org/10.1016/S0169-5347(03)00011-9.

Gardner, B. *European Agriculture: Policies, Production and Trade*. Routledge, London, 1996.

Germaine, S. S., and Wakeling, B. F. 2001. Lizard species distributors and habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biological Conservation*, 97(2): 229-237. https://doi.org/10.1016/S0006-3207(00)00115-4.

Grant, G. G. 1987. Copulatory behaviour of spruce budworm, *Choristoneura funiferana* (Lepidoptera: Tortricidae): experimental analysis of the role of sex pheromone and associated stimuli. *Annals of the Entomological Society of America*, 80(1): 78-88. https://doi.org/10.1093/aesa/80.1.78.

Harrison, S., and Gallandt, E. R. 2012. Behavioural Studies of *Harpalus rufipes* De Geer: an important weed seed predator in Northeastern US agroekosystems. *International Journal of Ecology*. Article number 846546. https://doi.org/10.1155/2012/846546.

Hobbs, R. J., Higgs, E. S., and Hall, C. M. *Novel ecosystems. Intervening in a New Ecological World Order*. Wiley-Blackwell, New Jersey, 2013.

Holec, V., Mišurcová, J., Tuf, I. H., and Veselý, M. 2006. Soil invertebrates (Coleoptera: Carabidae; Isopoda: Oniscidea) of the floodplain forest mosaic. Environmental changes and biological assessment III. *Scripta facultatis rerum naturalium Universitatis Ostravensis*, 163: 242-248.

Jeltsch, F., Blaum, N., Brose, U., Chipperfield, D. J., Clough, Y., Farwig, N., Geissler, K., Graham, H. C., Grimm, V., Hickler, T., Huth, A., May, F., Meyer, M. K., Pagel, J., Reineking, B., Rillig, C. M., Shea, K., Schurr, M. F., Schröder, B., Tielbörger, K., Weiss, L., Wiegand, K., Wiegand, T., Wirth, C., and Zurell, D. 2013. How can we bring together empiricists and modellers in functional biodiversity research? *Basic and Applied Ecology*, 14(2): 93-101. https://doi.org/10.1016/j.baae.2013.01.001.

Jenkinson, S. D. 2001. The impact of humans on the nitrogen cycle, with focus on temperate arable agriculture. *Plant and Soil*, 228: 3-15. https://doi.org/10.1023/A:1004870606003.

Kegel, B. Diurnal activity of carabid beetles living on arable land. In Stork, N. E., editors, *The Role of Ground Beetles in Ecological and Environmental Studies*, pages 65-76. Andover, Intercept, London, 1990.

Kenis, M., Auger-Rozenberg, M. A., Roques, A., Timms, L., Péré, C., Cock, M. J. W., Settele J., Augustin, S., and Lopez-Vaamonde, C. 2009. Ecological effects of invasive alien insects. *Biological Invasions*, 11: 21-45. https://doi.org/10.1007/s10530-008-9318-y.

Kim, K. H., and Pauleit, S. 2005. Landscape metrics to assess the ecological conditions of city regions: application to Kwangju City, South Korea. *International Journal of Sustainable Development and World Ecology*, 12(3): 226-244. https://doi.org/10.1080/13504500509469634.

Kingsolver, J., and Huey, R. B. 2008. Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, 10: 251-268.

Kratke, S. 2000. Berlin: the metropolis as a production space. European Planning Studies, 8: 7-27. https://doi.org/10.1080/096543100110901.

Kueffer, C., Pyšek, P., and Richardson, D. M. 2013. Integrative invasion science: Model systems, multi-site studies, focused meta-analysis, and invasion syndromes. *New Phytologist*, 200(3): 615-633. https://doi.org/10.1111/nph.12415.

Kueffer C. Ecological Novelty: Towards an Interdisciplinary Understanding of Ecological Change in the Anthropocene. In Greschke, H., and Tischler, J., editors, *Grounding Global Climate Change*, pages 19-37, Springer, Dordrecht, 2015. https://doi.org/10.1007/978-94-017-9322-3_2.

Kühn, I., Brandl, R., and Klotz, S. 2004. The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, 6: 749-764.

Kyba, C. C. M., Kuester, T., and Kuechly, U. H. 2017a. Changes in outdoor lighting in Germany from 2012-2016. *International Journal of Sustainable Lighting*, 19(2): 112-123. https://doi.org/10.26607/ijsl.v19i2.79.

Kyba, C. C. M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, D. C., Gaston, J. K., and Guanter, L. 2017b. Artificially lit surface of Earth at night increasing in radiance and extent. *Science Advances*, 3: e1701528. https://doi.org/10.1126/sciadv.1701528.

Landesamt für Umwelt Brandenburg (LfU) 2009. Flächendeckende Biotop- und Landnutzungskartierung (BTLN) im Land Brandenburg – CIR-Biotoptypen 2009. Available at: https://lfu.brandenburg.de/cms/detail.php/bb1.c.359429.de. Last accessed 02 March 2020.

Liu, Z., He, C., and Wu, J. 2016. The relationship between habitat loss and fragmentation during urbanization: An empirical evaluation from 16 world cities. *PLoS ONE,* 11(4): e0154613. https://doi.org/10.1371/journal.pone.0154613.

Liu, S. H., Sylvia, P., and LI, X. B. 2002. Spatial patterns of urban land use growth in Beijing. *Journal of Geographical Sciences*, 12: 266–274. https://doi.org/10.1007/BF02837544.

Lurgi, M., López, B. C., and Montoya, J. M. 2012. Novel communities from climate change. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 367(1605): 2913-2922. https://doi.org/10.1098/rstb.2012.0238.

Maas, S., Detzel, P., and Staudt, A. *Gefährdungsanalyse der Heuschrecken Deutschlands - Verbreitungsatlas, Gefährdungseinstufung und Schutzkonzepte.* Bundesamt für Naturschutz, Landwirtschaftsverlag, Münster-Hiltrup, 2002.

McGeoch, M. A. 1998. The selection, testing and application of terrestrial insects as bioindicators. – *Biological Reviews of the Cambridge Philosophical Society* 73(2): 181-201. https://doi.org/10.1111/j.1469-185X.1997.tb00029.x.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127(3): 247-260. https://doi.org/10.1016/j.biocon.2005.09.005.

McKinney, M. L. 2008. Effects of urbanisation on species richness: A review of plants and animals. *Urban Ecosystems*, 11: 161-176. https://doi.org/ 10.1007/s11252-007-0045-4.

Merckx, T., Kaiser, A., and Van Dyck, H. 2018. Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Global Change Biology*, 24(8): 3837-3848. https://doi.org/10.1111/gcb.14151.

Millennium Ecosystem Assessment. *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, 2005.

Muchovej, M. C. R., and Rechcigl, E. J. Soil processes and water quality. In Steward, A. B., editor, *Nitrogen fertilizer effects on water quality*, pages 111-113. CRC Press, Boca Raton, 1994.

Niemeier, S., Müller, J., Struck, U., and Rödel, M-O. 2020. Superfrogs in the city: 150 year impact of urbanization and agriculture on the European Comon Frog. *Global Change Biology*, 26(12): 6729-6741. https://doi.org/10.1111/gcb.15337.

Nieminen, M., Rita, H., and Uuvana, P. 1999. Body size and migration rate in moths. *Ecography*, 22(6): 697-707. https://doi.org/10.1111/j.1600-0587.1999.tb00519.x.

Noss, R. F. 1990. Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology*, 4(4): 355-364. https://doi.org/10.1111/j.1523-1739.1990.tb00309.x.

Oduor, M. O. A., Leimu, R., and van Kleunen, M. 2016. Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. *Journal of Ecology*, 104(4): 957-968. https://doi.org/10.1111/1365-2745.12578.

Oke, T. R. 1973. City size and the urban heat island. *Atmospheric Environment*, 7(8): 769-779. https://doi.org/10.1016/0004-6981(73)90140-6.

Owens, S. C. A., Cochard, P., Durrant, J., Farnworth, B., Perkin, K. E., and Seymoure, B. 2020. Light pollution is a driver of insect decline. *Biological Conservation*, 241: 108259. https://doi.org/10.1016/j.biocon.2019.108259.

Palkovacs, E. P., Kinnison, T. M., Correa, C., Dalton, M. C., and Hendry, P.A. 2011. Fates beyond traits: Ecological consequences of human-induced trait change. *Evolutionary Applications*, 5(2): 183-191. https://doi.org/10.1111/j.1752-4571.2011.00212.x.

Pamme, H. *Das Politikfeld Umweltpolitik - Politikfeldbezogene Verwaltungsanalyse*. Springer, Wiesbaden, 2003.

Peck, L. S., Mcquaid, B., and Campbell, C. L. 1998. Using ant species (Hymenoptera: Formicidae) as a biological indicator of agroecosystem condition. *Environmental Entomology*, 27(5): 1102-1110. https://doi.org/10.1093/ee/27.5.1102.

Peterson, B. J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology, Evolution and Systematics*, 18: 293-320. https://doi.org/10.1146/annurev.es.18.110187.001453.

Pyšek, P. Approaches to studying spontaneous settlement flora and vegetation in central Europe. In Sukopp, H., Numata, M., and Huber A., editors, *Urban Ecology as the Basis of Urban* Planning, pages 23-39. SPB Academic Publishing, The Hague, 1995.

Ramankutty, N., Evan, A. T., Monfreda, C., and Foley, J. A. 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles* 22(1): GB1003. https://doi.org/10.1029/2007GB002952.

Rich, C., and Longcore, T. *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington, 2006.

Rocha, A. L., Aleixo, A., and Allen, G., et al. 2014. Specimens collection: An essential tool. *Science*, 344(6186): 814-815. https://doi.org/10.1126/science.344.6186.814.

Rosing, M. N., Ben-David, M., and Barry, P. R. 1998. Analysis of stable isotope data: A K Nearest-Neighbors Randomization Test. *The Journal of Wildlife Management*, 62(1): 380-388. https://doi.org/10.2307/3802302.

Rutowski, R. L., Gislén, L., and Warrant, E. J. 2009. Visual acuity and sensitivity Increase allometrically with body size in butterflies. *Arthropod Structure and Development*, 38(2): 91-100. https://doi.org/10.1016/j.asd.2008.08.003.

Schowalter, T.D. *Insect Ecology. An ecosystem approach*. Elsevier, Amsterdam, 2000.

Senate Department for Urban Development and Housing (SenUDH) 2014. Berlin Environmental Atlas. 05.08 Biotope Types. Available at: https://www.stadtentwicklung.berlin.de/umwelt/umweltatlas/ek508.htm. Last accessed on 27 March 2020.

SenStadtWohn (Senatsverwaltung für Stadtentwicklung und Wohnen Berlin) 2018. *Langjährige Entwicklung der Luftqualität*. Available at: https://www.stadtentwicklung.berlin.de/umwelt/umweltatlas/d312_03.htm Last accessed 18 September 2019.

Slade, E. M., Merckx, T., Riutta, T., Bebber, D. P., Redhead, D., Riordan, P., and Macdonald, D. W. 2013. Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology*, 94(7): 1519–1530 https://doi.org/10.1890/12-1366.1.

Song, P-X., Hansen, C. M., Stehman, V. S., Potapov, V. P., Tyukavina, A., Vermote, F. E., and Townshend, R. J. 2018. Global land change from 1982 to 2016. *Nature*, 560: 639-643. https://doi.org/10.1038/s41586-018-0411-9.

Sotherton, W. N., and Self, J. M. Changes in plant and arthropod diversity on lowland farmland: An overview. In Aebischer, J. N., editor, *The Ecology and Conservation of Lowland Farmland Birds*, pages 26-35. British Ornithologists' Union, Hertfordshire, 2000.

Soundranayagam, J. P., Sivasubramanian, P., Chandrasekar, N., Duraira, K. S. P. 2011. An analysis of land use pattern in the industrial development city using high resolution satellite imagery. *Journal of Geographical Science*, 21: 79-88. https://doi.org/10.1007/s11442-011-0830-0.

Smith, H. V. 2003. Eutrophication of freshwater and coastal marine ecosystems: A global problem. *Environmental Science and Pollution Research*, 10: 126-139. https://doi.org/10.1065/espr2002.12.142.

Stange, E. E; and Ayres, M. P. Climate Change Impacts: Insects. In: *Encyclopedia of Life Sciences* (ELS). John Wiley & Sons, Chichester, 2010. https://doi.org/10.1002/9780470015902.a0022555 2010.

Steffen, W., Sanderson, A., Tyson, P. D., Jäger, J., Matson, P. A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H. J., Turner II, B. L., and Wasson, R. J. *Global Change and the Earth System. A planet under pressure*. Springer, Berlin, 2004.

Steffen, W., Grinevald, J., Crutzen, P., and McNeill, J. 2011. The Anthropocene: Conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Science*, 369(1938): 842-867. https://doi.org/10.1098/rsta.2010.0327.

Sukhodolskaya, R. A. 2013. Intraspecific body sizes variation in ground beetles (Coleoptera, Carabidae) in urban–suburban–natural gradient. *Acta Biologica Universitatis Daugavpiliesis*, 13(1): 121-128. ISSN 1407-8953.

Sukopp, H., and Werner, P. Urban environments and vegetation. In Holzner, W., Werger, A. J. M, and Ikusima, I., editors, *Man's Impact on Vegetation*, pages 247-260, Dr. W. Junk Publishers, The Hague, 1983.

Sunderland, K. D., Loevei, G. L., and Fenlon, J. 1995. Diets and reproductive phenologies of the introduced ground beetles *Harpalus affinis* and *Cilvina australasiae* (Coleoptera: Carabidae) in New Zealand. *Australian Journal of Zoology*, 43(1): 39-50. https://doi.org/10.1071/ZO9950039.

Sutton, P. C. A. 2003. A scale adjusted measure of 'urban sprawl' using nighttime satellite imagery. *Remote Sensing of Environment*, 86(3): 353-369. https://doi.org/10.1016/S0034-4257(03)00078-6.

Szentkirályi, F., Bernáth, B., Kádár, F., and Retezár, I. 2003. Flight of ground beetles towards polarized and unpolarised light sources. *European Carabidology*, 114: 313-324.

Thiele, H.U. Carabid beetles in their environments. In *Zoophysiology and Ecology*, Vol. 10, pages 1-192. Springer, Berlin, 1977.

Thornhill, R., and Alcock, J. *The evolution of insect mating systems*. Harvard University Press, Cambridge, 1983.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, H. W., Simberloff, D., and Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. *Science*, 292(5515), 281-284. https://doi.org/10.1126/science.1057544.

Tockner, K., Pusch, M., Gessner, J., and Wolter, C. 2011. Domesticated ecosystems and novel communities: Challenges for the management of large rivers. *Ecohydrology and Hydrobiology*, 11(3-4): 167–174. https://doi.org/10.2478/v10104-011-0045-0.

Townsend, J. I. 1992. *Harpalus affinis* (Schrank) (Coleoptera: Carabidae) recently established in the North Island of New Zealand. *New Zealand Entomology*, 15(1): 25-29. https://doi.org/10.1080/00779962.1992.9722624.

Trautner, J. *Die Laufkäfer Baden-Württembergs*, Band 2: Spezieller Teil II, Synoptisher. Ulmer, Stuttgart, 2017.

Tseng, M., Kaur, K. M., Pari, S. S., Sarai, K., Chan, D., Yao, C. H., Porto, P., Toor, A., and Toor, H. S. 2018. Decrease in beetles body size linked to climate change and warming temperatures. *Journal of Animal Ecology*, 87(3): 647-659. https://doi.org/10.1111/1365-2656.12789.

Turner, B. L., and Clark, W. C. *The Earth as Transformed by Human Action*. Cambridge University Press, Cambridge, 1990.

UBA. *Umweltdaten Deutschland*. Umweltbundesamt. Erich Schmidt, Berlin, 1998.

UNEP/WHO. *City air quality trends*, Vol. 2., WHO PEP/93 26, UNE93 26P GEMS 93.A.2, Geneva, 1993.

United Nations, Department of Economic and Social Affairs, Population Division. *World Urbanization Prospects*: The 2018 Revision (ST/ESA/SER.A/420). United Nations, New York, 2019.

Van Langevelde, F., Ettema, A. J., Donners, M., WallisDeVries, F. M., and Groenendijk, D. 2011. Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, 144(9): 2274-2281. https://doi.org/10.1016/j.biocon.2011.06.004.

Van't Hof, A., Edmonds, E., Dalikova, M., Marec, F., and Saccheri, J. I. 2011. Industrial melanism in British Peppered Moths has a singular and recent mutational origin. *Science* 332(6032): 958-960. https://doi.org/10.1126/science.1203043.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. 1997. Human domination of earth's ecosystems. *Science*, 277(3525): 494-499. https://doi.org/ 10.1126/science.277.5325.494.

Waddington, H. C. 1959. Evolutionary adaptation. *Perspectives in Biology and Medicine*, 2(4): 379-401. https://doi.org/10.1353/pdm.1959.0027.

Weller, B., and Ganzhorn, U. J. 2003. Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. *Basic and Applied Ecology*, 5(2): 193-201. https://doi.org/10.1078/14391791-00220.

Wey, K-G. *Umweltpolitik in Deutschland - Kurze Geschichte des Umweltschutzes in Deutschland seit 1900*. Westdeutscher Verlag, Opladen, 1982.

Wrase, D. W. Harpalina in Die Käfer Mitteleuropas: In Freude, Harde, W. K., Lohse, A. G., Klausberger, B., and Müller-Motzfeld, G., editors, *Adephaga 1 Carabidae (Laufkäfer)*, volume 2, Spektrum, Heidelberg, 2004.

Zerbe, S., Maurer, U., Schmitz, S., and Sukopp, H. 2002. Biodiversity in Berlin and its potential for nature conservation. *Landscape and Urban Planning*, 62: 139-148. https://doi.org/10.1016/S0169-2046(02)00145-7.

Zhu, W-X., Dillard, D. N., and Grimm, B. N. 2004. Urban nitrogen biogeochemistry: Status and process in green retention basins. *Biogeochemistry*, 71: 177-196. https://doi.org/10.1007/s10533-004-9683-2.

Ziegler, J. 2011. Recent range extensions of tachinid flies (Diptera: Tachinidae, Phasiinae) in north-east Germany and a review of the overall distribution of five species. *Studia Dipterologica*, 18: 29-54.

5. Papers

5.1 Paper 1

Impact of light pollution on moth morphology – a 137-year study in Germany

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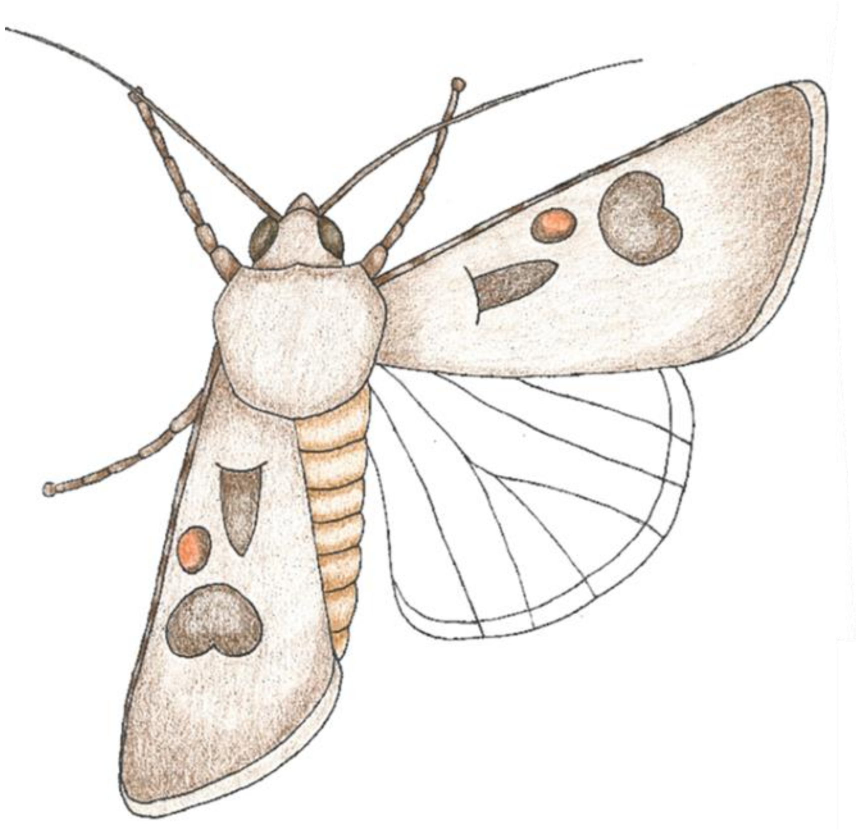

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Impact of light pollution on moth morphology—A 137-year study in Germany

Silvia Keinath[a,b,*], Franz Hölker[c,d], Johannes Müller[a,b], Mark-Oliver Rödel[a,b]

[a]*Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, Berlin 10115, Germany*
[b]*Berlin-Brandenburg Institute of Advanced Biodiversity Research—BBIB, Königin-Luise-Str. 2-4, Berlin 14195, Germany*
[c]*Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, Berlin 12587, Germany*
[d]*Institute of Biology, Freie Universität Berlin, Berlin 14195, Germany*

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Abstract

Increasing artificial illumination during night has multifaceted effects on species. Moths are shown to be distracted and attracted by artificial light sources, leading to increased mortality through predation or exhaustion. Increased mortality can be expected to increase selection pressure on morphology, particularly those being functional in light detection and flight ability. We were thus interested if intraspecific traits differ between areas and times with differing light pollution values. We chose the moth *Agrotis exclamationis*, a common species in the Berlin-Brandenburg region, Germany, a region that offers very different levels of light pollution across space and time. We examined body length, eye size and forewing length, traits likely targeted through selection due to light pollution. We examined moths collected over the past 137 years. We predicted decreasing forewing length, body and eye size, in response to increasing light pollution and expected to see trait changes from the past to today, and from rural to urban areas, representing temporal and spatial gradients of increasing light pollution. In order to determine current levels of light pollution, we used radiance values of the years 2012 to 2019. These values were the base to extrapolate previous radiance values for all sample sites and years. We observed no trait differences along the spatial gradient, but trait and sex dependant changes along the temporal gradient. We could not confirm a direct causal link between changes in body size and female eye size. However, we revealed indirect effects of light pollution, and assume habitat fragmentation and host-plants to be the main drivers for these effects. A trend towards smaller-eyed females in ‘medium’ and ‘high’ light-polluted areas over time could be a first indication that morphological trait changes to light pollution are taking place.

Keywords: *Agrotis exclamationis*; Radiance; Morphological traits; Body length; Eye size; Wing length; Anthropogenic gradient

Introduction

Artificial light at night (ALAN) is widespread, positively correlated with urbanisation (Sutton, 2003), and increases at an annual rate of about 2–6% worldwide (Hölker et al.,

*Corresponding author.
E-mail addresses: silvia.keinath@mfn.berlin (S. Keinath), hoelker@igb-berlin.de (F. Hölker), Johannes.Mueller@mfn.berlin (J. Müller), mo.roedel@mfn.de (M.-O. Rödel).

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2010a; Kyba et al., 2017b). Because ALAN has been introduced in places, times and at intensities at which it does not naturally occur, it became a threat to biodiversity (Gaston, Visser & Hölker, 2015; Hölker, Wolter, Perkin & Tockner, 2010b; Longcore & Rich, 2004), with respective ecological and evolutionary consequences (Hopkins, Gaston, Visser, Elgar & Jones, 2018; Navara & Nelson, 2007; Rich & Longcore, 2006). Insects, especially moths, seem to be particularly affected by ALAN (Owens et al., 2020; Van Langevelde, Ettema, Donners, WallisDeVries & Groenendijk, 2011). In clear nights moths use celestial light sources such as moon and stars for orientation (e.g. Baker & Sadovy, 1978). However, they get distracted by artificial light and often stay trapped flying around lamps. There they become easy prey to predators or simply die by exhaustion (Degen et al., 2016; Eisenbeis, 2006). Natural selection thus should favour individuals that are less attracted by artificial light sources (Gaston, Bennie, Davies & Hopkins, 2013), as it was shown for populations of ermine moths Yponomeuta cagnagella, where specimens from urban areas show a reduced flight-to-light behaviour compared to conspecifics from pristine dark-sky habitats (Altermatt & Ebert, 2016). Morphological trait changes that reduce flight-to-light behaviour may thus indicate adaptation to ALAN in moths. Flight ability is important to meet mates, disperse, escape from predators, and search for nectar and larval host-plants (Chai & Srygley, 1990; Scoble, 1992). Longer-winged specimens have better flight abilities than shorter-winged ones (Beall & Williams, 1945); and larger specimens have been shown to be better dispersers than smaller ones (Nieminen, Rita & Uuvana, 1999; Slade et al., 2013). Specimens with better flight abilities might be relatively more often attracted by ALAN, because they cover larger distances and thus the chances that they come close to artificial light increases (Van Langevelde et al., 2011). Visual cues are important for navigation strategies (Wehner, 1984). Although males' mate detection is primarily based on sex pheromones, visual cues are additively used for short-distance detection (Grant, 1987). In females visual cues are important for selecting host-plants for oviposition (Bernays, 2001). Moth's eye size likewise impacts sensitivity to light (Yack, Johnson, Brown & Warrant, 2007). For instance, Rutowski, Gislén and Warrant (2009) showed that large moths with relatively larger eyes have more accurate and more sensitive vision than smaller individuals, and, species with larger eyes are usually more affected by artificial light than smaller eyed ones (Van Langevelde et al., 2011). Thus, increasing ALAN may select for smaller-eyed individuals.

Because trait change takes place across many generations, it is difficult to observe respective processes within usual study periods. However, this challenge might be overcome by examining museum vouchers, which have been collected over long periods (Doudna & Danielson, 2015; Keinath, Frisch, Müller, Mayer & Rödel, 2020; Niemeier, Müller, Struck & Rödel, 2020). Herein we investigated the moth Agrotis exclamationis. During the last 137 years this species was regularly collected in the German Berlin-Brandenburg area, a region exhibiting steep temporal and spatial gradients of light pollution. We hypothesize a decrease in body size, relative forewing length and eye size due to less mobility and sensitive vision from low to high levels of light pollution, in space and time (Fig. 1).

Materials and methods

Study area

Berlin, Germany, is an increasingly urbanizing city (Antrop, 2000), including growing levels of light pollution (Kyba et al., 2017b). In contrast, the federal state of Brandenburg, a rural area surrounding Berlin, is mostly consisting of agricultural and near-natural environments (Antrop, 2000; Cochrane & Jonas, 1999). Industrialization in Berlin started in the beginning of the 19th century (Ribbe, Bohm, Schich & Schulz, 2002a). Streets and public places became first artificially illuminated in 1882 (Haubner, 1962). Berlin's population was steadily increasing and reached an unrivalled peak in the 1920s (Ribbe, Bohm, Schich & Schulz, 2002b), comprising a much lower human population after World War II (Ribbe et al., 2002b). Since an economic boom starting in the 1950s onward, the human population and the density and intensity of artificial light increased (Eisenbeis & Hänel, 2009; United Nations, 2002). For instance, Kyba, Kuester and Kuechly (2017a) demonstrated an increase of lit areas of 2.5% and an increase in radiance of 7.4% in already lit areas from 2012 to 2016.

Study species

Agrotis exclamationis (Linnaeus, 1758) (Lepidoptera, Noctuidae) is common and widespread in our study region, at least over the past 137 years. It is a nocturnal pollinator, exhibiting forewing length of 15 to 19 mm s and occurs in grasslands, parks, gardens, glades, ruderal sites, and on forest edges, rarely at clearings. It is widespread from Europe to Asia, and produces two generations from May to July, and from August to September, the latter comprising smaller individuals (Ebert, Rennwald & Bartsch, 1997). We only examined imagines from the first generation to ensure comparable traits. Relative to migratory moths, *Agrotis exclamationis* is a medium mobile species. Jones, Lim, Bell, Hill and Chapman (2016) show that males cover distances of up to 6935 m. Females deposit their eggs on host-plants (Xu, Liu & Zhang, 2013). Larvae are generalist feeders (Ebert, Rennwald & Bartsch, 1997), and may become crop and potato pests (Xu et al., 2013). Sexes can be distinguished by feathered antennae in males, and string-shaped antennae in females (Ebert et al., 1997).

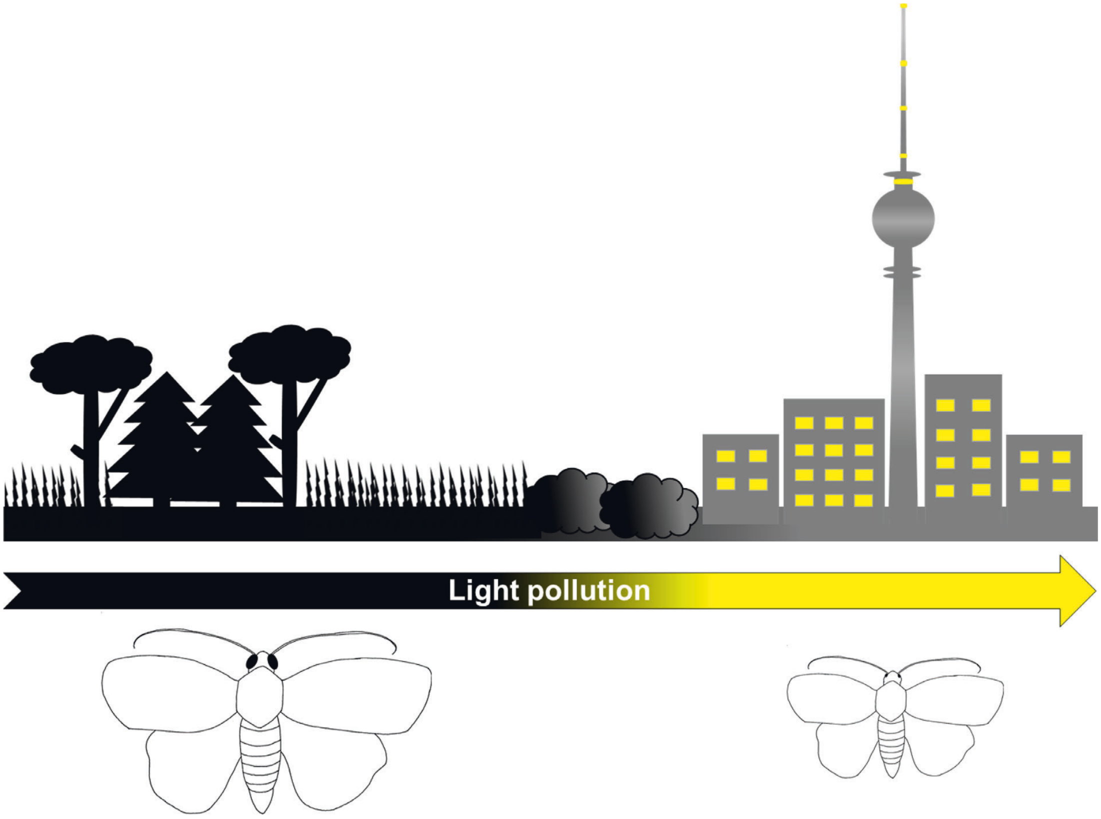

Fig. 1. Hypothetic influence of increasing light pollution on moths' morphological traits. We expect that larger moths with relatively larger eyes and forewing length will occur at sites and in times with low levels of light pollution. With increasing light pollution, we expect a decrease in body size, relative eye size, and forewing length.

Origin of specimens

In total, we examined 79 *A. exclamationis* (48 females; 31 males), including 37 from the city of Berlin and 41 from the federal state of Brandenburg; 54 specimens (29 females; 25 males) were museum vouchers (Museum für Naturkunde, Berlin and Naturkundemuseum Potsdam), spanning the years 1880 to 1998; 25 specimens (19 females; 6 males) were collected in 2017. Museum vouchers from Berlin were collected in parks, small green spaces, industrial areas and lakefronts. Vouchers from ruderal Brandenburg were collected around small villages and within larger towns. Museum labels mentioned that vouchers were collected with light traps. Recently collected specimens were captured manually by black light traps on 18 dry grassland sites within Berlin and two dry grassland sites in Brandenburg (June to July 2017) (see Appendix C: Table 1). We assume that museum vouchers were manually picked from light traps for the respective collections (no passive collection for ecological studies). Because our species is known to be mainly attracted by short-wavelengths (Fayle, Sharp & Majerus, 2007; Somers-Yeates, Hodgson, McGregor, Spalding & Ffrench-Constant, 2013) samples from 'white' (with a high proportion of blue light) and 'black' lights traps (UV and blue light) should be comparable.

Measurements

Specimens were pinned planar in drawers. Complete drawers with all specimens were scanned with a SatScan™ imaging system developed by SmartDrive Ltd., including a camera with a 0.16x telecentric lens. The camera moves along rails positioned above the drawer and captures 240 images at precise positions. These images are then 'stitched' with SatScan analyse 64 software to produce a single high-resolution image of the entire drawer (Johnson, Mantle, Gardner & Backwell, 2013). Body length, and forewing length measures were taken from these figures using the ruler tool in Adobe Photoshop (Version: CS 5.1). Standardized body length (SBL) measures were taken with modifications following Kavanaugh (1979). SBL commonly comprises head length, thorax length and abdominal length. We measured abdominal length by summing up all 10 single segment measures of the abdomen by using the maximum distance because abdomens of some vouchers were curved to one side. For better measures of some segments that were partly covert by other segments, we used polygon lasso and magic lasso tools to uncover them. Forewing length (FWL) were measured from the anterior axillaria joint of the forewing with the thorax along the costa contact with parapteron episternale to the tip of the forewing. Horizontal diameters of the eyes were measured with a measuring ocular attached to a dissecting microscope (Leica MZ 12) (see Appendix A). Measurement errors were determined by the mean of a randomized chosen subsample of 10 specimens (accuracy was: SBL: ± 0.03 mm; FWL: ± 0.06 mm; eye diameter: ± 0.03 mm). The data used in the analyses were standardized to SBL: relative mean diameter of the left and right eye (eye diameter / SBL), and the relative mean length of the left and right forewings (FWL / SBL).

Data classification

For categorization of ALAN levels at different sites and years, we used the "light pollution map" (www.lightpollutionmap.info) (Light pollution map, 2019), based on satellite data from the defense Meteorological Satellite Program-Operational Linescan System (DMSP; 1992 to 2011; spatial resolution: 5 × 5 km), and the Visible Infrared Imaging Radiometer Suite Day-Night Band (VIIRS DNB; 2012 to 2019; spatial resolution: 750 × 750 m, see Miller et al., 2013). Especially VIIRS DNB has been shown to have sufficient resolution to identify major sources of waste light (Kyba et al., 2015). The maps based on VIIRS DNB data were used to display radiance values (10^{-9} W / cm^2 * sr) for every verified moth collection site. In contrast, maps based on DMSP data are classified into light categories. The higher spatial resolution of DMSP and VIIRS DNB pixel between different years are sufficient for our analyses because they match the accuracy of the museum label data, usually given on Berlin district levels, districts usually being even larger than the spatial resolution of DMSP pixel.

For moths collected in 2017, we used absolute radiance values of their respective sampling sites. For moths collected in previous years (1880 to 2010), we calculated for each collection site the mean relative rate of ALAN increase over the years 2012 to 2019 from maps that are covered by VIIRS DNB. With these site-specific ALAN increase rates over seven years, we back-calculated the ALAN levels of former years, using time steps of seven years (see Appendix C: Table 1). To evaluate the reliability of this approach, we validated our calculated radiance values with the map based on DMSP data from 1998 to 2005. All retrospectively calculated radiance levels were within the given intervals of the DMSP light categories of the respective year.

In a next step we established our own Light Pollution Categories (LPC) of both measured and back-calculated radiance values. Category 1 'low' is spanning radiance values from 0 to 0.25; category 2 'medium' from 0.25 to 1.50 and category 3 'high' from 1.5 to 50.0 (10^{-9} W / cm^2 * sr). We used 'LPC' for spatial analyses and temporal analyses for investigating effects of light pollution on a larger scale.

Statistical analysis

For all analyses we used software of the R-Project, version 3.6.3 (R Core Team, 2020). For testing normal distribution of 'Radiance' values, we used Shapiro Wilk tests. For non-normally distributed data, we used Spearman correlations, testing for correlation between 'Radiance' and 'Year' for the entire study region Berlin-Brandenburg ('Radiance' ~ 'Year') to get a rough overview of the ALAN situation in the entire region; and separately for the different areas Berlin ('Radiance Berlin' ~ 'Year') and Brandenburg ('Radiance Brandenburg' ~ 'Year'), respectively.

We tested distribution of our response variables ('SBL'; 'eye diameter / SBL' and 'FWL / SBL') by visualisation via QQPlot with the R packages 'carData' (Fox, Weisberg & Price, 2019) and 'MASS' (Venables & Ripley, 2002). With normal distribution, fitting our data best, we ran linear regression models for temporal analyses. We used 'Radiance', 'Year' and 'Sex' as factors, tested the interaction between 'Year' and 'Radiance' (Lm = 'Trait' ~ 'Year' * 'Radiance' + 'Sex'), and did the same for testing 'Light Pollution Categories' (LPC) (Lm = 'Trait' ~ 'Year'* 'LPC' + Sex).

For spatial analyses we used one-way analyses of variance (ANOVA), separately for sexes, by using 'LPC' as grouping variable ('Trait' ~ 'LPC'). We used Pearson correlations, testing for correlation between 'SBL' and 'Year' and between 'eye diameter / SBL' and 'Year', both separately for males and females. For visualization, we used ggplot2 with the R-package ggplot2 (Wickham, 2016).

Results

The Spearman correlation between 'Radiance' and 'Year' for the entire study region, Berlin-Brandenburg, was significant (S = 31,308; rho = 0.619; $p < 0.001$), indicating a continuous increase of light pollution over time. This correlation was equally significant for the sub-regions, although the correlations were weaker; Berlin: S = 5505.6; rho = 0.398; p = 0.013; and Brandenburg: S = 6664.1; rho = 0.420; p = 0.006 (Fig. 2).

We detected no significant effect of 'Radiance' on any of the investigated traits. However, body size differed between sexes (Lm: df = 74; t = −4.070; $p < 0.001$) and changed over years (Lm: df = 74; t = 2.402; p = 0.019). Size of both sexes was significantly positively correlated with 'Years' (Pearson correlation: females: t = 2.687; df = 46; R^2 = 0.368; p = 0.010; males: t = 2.348; df = 29; R^2 = 0.400; p = 0.026), i.e. body size increased over time but not in response to 'Radiance' (Fig. 3A). Likewise, relative eye size differed between sexes (Lm: df = 74; t = 7.757;

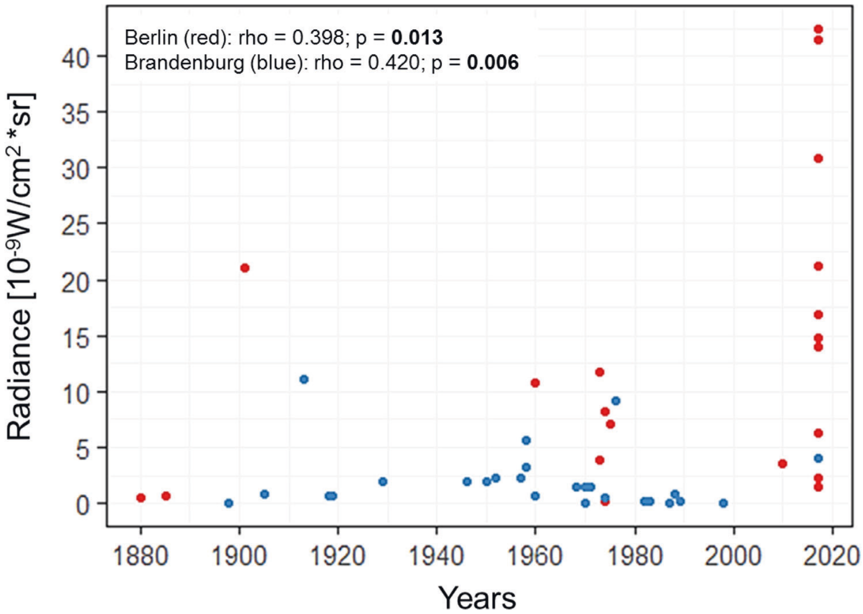

Fig. 2. Radiance values taken from the light pollution maps for the year 2017 (www.lightpollutionmap.info), and back-calculated radiance values for the years 1880 to 2010 for moth collecting sites from the Berlin-Brandenburg region, Germany. Significant *p*-values of Spearman correlation are given in bold.

$p < 0.001$), and changed over years (Lm: df = 74; $t = -2.474$; $p = 0.016$). Females' eye size was significant negatively correlated with 'Years' (Pearson correlation: $t = -2.502$; df = 46; R2 = −0.346; $p = 0.016$), whereas the negative correlation in males' eye size between 'Years' was non-significant. Thus, females' relative eye size decreased over time but again, not in response to 'Radiance' (Fig. 3B). Relative forewing length did not differ between sexes and did not change over years (see Appendix B: Table 1).

We found no significant effect of 'Light Pollution Categories' (LPC) ('high'; 'medium' and 'low') on any of the investigated traits in our temporal analyses. However, there was a trend for relative eye size (Lm: df = 74; $t = -1.949$; $p = 0.055$), indicating smaller-eyed females in 'medium' and 'high' LPCs compared to 'low' LPCs (Fig. 4). The interaction between 'LPC' and 'Year' indicated also a trend (Lm: df = 74; $t = 1.988$; $p = 0.051$), showing that increasing 'LPCs' across years have an influence on the trend of decreasing eye size (see Appendix B: Table 2). We found no significant effect in our spatial analysis. Body size, relative eye size and forewing length did not differ between areas with 'low', 'medium' and 'high' light pollution categories. This absence of any effects was detected in males as well as in females (see Appendix B: Table 3).

Discussion

Increasing artificial light at night (ALAN) is known to have consequences on nocturnal moths, because they are distracted by artificial light. Therefore, natural selection should favour individuals that are less impacted by ALAN (Van Langevelde et al., 2011), what could lead to intraspecific morphological trait changes.

In our study we focused on spatio-temporal changes in body size, relative eye size and forewing length in the moth *Agrotis exclamationis* in response to different ALAN levels within the Berlin-Brandenburg area, Germany. We predicted smaller-sized specimens with relatively shorter forewings and smaller eye size in areas and times with high levels of ALAN than in less impacted areas and times.

Generally, we observed that *A. exclamationis* displayed sexual dimorphism in body and relative eye size, but not in forewing length. Body size increased in both sexes, whereas relative eye size decreased only in females over the past 137 years. Both effects could not be verified as a direct response to ALAN. However, we detected a trend towards smaller eye size in females when ALAN levels increased over time. No changes were observed in forewing length in both sexes over time, and no differences occurred in any trait along the spatial gradient.

The lack of trait changes in response to increasing ALAN across space and time was unexpected and needs explanation. First, all of our specimens were captured with light traps. Thus, our specimens may have shown a pronounced flight-to-light behaviour, whereas we may have missed individuals with a reduced flight-to-light behaviour. Only a light-independent collecting method like pheromone traps, traps based on floral compounds (Tóth et al., 2010) or malaise traps (Hallmann et al., 2017) might clarify that point. However, such vouchers were not available.

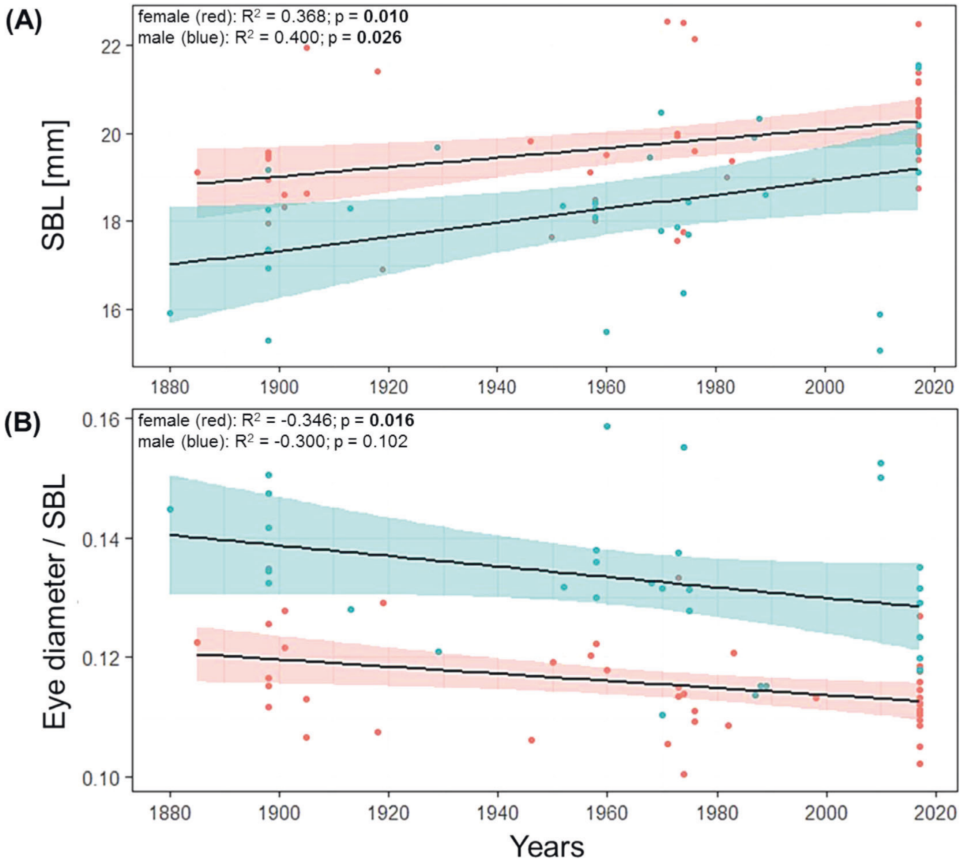

Fig. 3. Morphological trait change in *Agrotis exclamationis* over years. (A) body size (SBL), and (B) eye diameter (eye diameter / SBL) over the years 1880 to 2017 with red or light grey (females) and blue or dark grey (males) confidence intervals and smoothed regression lines from linear models and Pearson correlation coefficients. Significant p-values are given in bold. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

Another reason for the absence of effects in response to increasing ALAN across time might be due to our study's timeframe. Although it is known that intraspecific morphological trait change in response to human induced environmental changes may arise across relatively short timeframes in insects (Keinath et al., 2020; Van't Hof, Edmonds, Dalikova, Marec & Saccheri, 2011), and even vertebrates (Doudna & Danielson, 2015; Niemeier et al., 2020), most evolutionary processes are depending on longer times than our 137 years study period. However, in another moth intraspecific behavioural adaptations in reduced flight-to-light behaviour apparently already took place in urban areas (Altermatt & Ebert, 2016); as a consequence, morphological trait changes might follow.

A further reason for the lack of any light-driven trait changes could be due to inaccuracy of our retrospectively computed rates of ALAN. The further back the radiance calculations reached, the less certain these values might be. For instance, we based our calculations on the ass, umption of continuous change. However, ALAN levels were already high during the economic boom in the 1920s (Ribbe et al., 2002b), followed by a drastic decrease during World War II. Furthermore, the spectral quality of ALAN changed over time, due to the application of different light sources (Gaston, Davies, Bennie & Hopkins, 2012; Kyba et al., 2015). Finally, the accuracy of localities on labels and thus our assignment of light intensity might have failed to reach the necessary precision, as even on a relatively small-scale light intensity can vary a lot (Kuechly et al., 2012).

An indirect hint that increasing ALAN influences our study species would be a decline in *A. exclamationis'* abundance over time in areas with high ALAN impact, and a stable population in less impacted areas. Unfortunately, such data are not available. However, Conrad, Warren, Fox, Parsons and Woiwod (2006) show a decline in *A. exclamationis* across 35 years in lit areas of Britain, and discuss increasing ALAN as one a responsible factor.

We believe that our assumptions of ALAN impacting our study species are realistic. When examining changes in

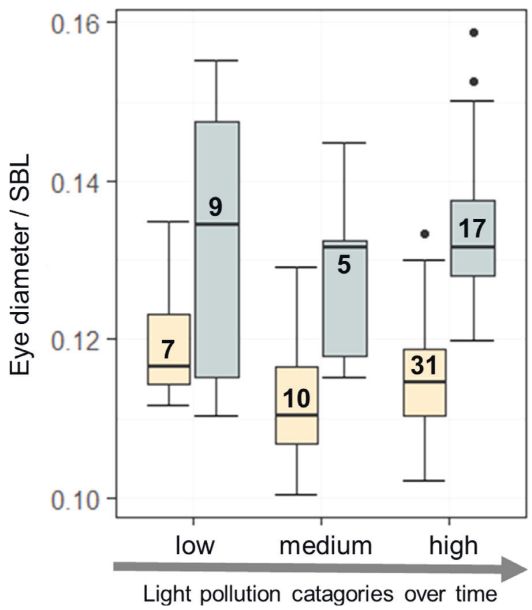

Fig. 4. Mean diameter of right and left eyes in relation to Standardized Body Size (eye diameter / SBL) over time (arrow) with different light pollution categories (low, medium, high) of females (reddish or light grey boxplots) and males (blue or dark grey boxplots). Numbers within boxplots give sample sizes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

response to Light pollution categories (LPC), we indeed found a trend towards smaller-eyed females in 'medium' and 'high' light polluted areas over time. These categories are larger-scaled than radiance values and could make changes more visible. We interpret this trend as a first indicator that morphological trait changes in response to ALAN are already taking place (compare Van Langevelde et al., 2011).

However, it remains to be discussed why this trend was only found in females and not in males. During our most recent sampling, more females were captured than males. This might be a hint that females are more sensitive to ALAN. In contrast, Williams (1939) could show that male *A. exclamationis* are significantly more often attracted by light traps, making this explanation unlikely. Moreover, we found a decrease in females' eye size across time but not verifiable in response to radiance values and not in males. Male moths have larger eyes than females (Yagi & Koyama, 1963) because they are depending on visual cues for detecting females in near distance (Grant, 1987). The change of male eye size might be opposed by other selection pressures, i.e. less effective escape from predators and/or mate detection. Females in Lepidoptera are indeed known to be less dependant on their eyes for mating, instead females use vision (amongst other senses) for host-plant detection and oviposition (Bernays, 2001). *Agrotis exclamationis* is a generalist and therefore depending on high sensory capacity because they have to recognize and choose between broader ranges on host-plants than specialists (Bernays & Wcislo, 1994; Dall & Cuthill, 1997; Levins & MacArthur, 1969). Interestingly, Callahan (1957) shows that the noctuid moth *Heliothis zea* seemed to be unable to recognize host-plants for oviposition when artificially illuminated, probably because light was reflected from green plants. Thus, in areas with high ALAN levels females' view on their host-plants might be impacted, favouring selection for females with smaller eyes which are less disrupted by ALAN. Additionally, a change of plant composition due to human-established plant species in our anthropogenically influenced study area (Sukopp & Werner, 1983; Zerbe, Maurer, Schmitz & Sukopp, 2002) could be a reason for females' decrease in eye size probably due to a diluting effect of their native, established host-plant species.

We also predicted body size and relative forewing length to become smaller with higher ALAN levels because specimens that are more mobile may encounter and consequently become distracted by artificial light more often (Chai & Srygley, 1990; Rutowski et al., 2009; Van Langevelde et al., 2011). Our findings revealed increased body size in both sexes over time, but not in response to ALAN. We found no changes in forewing length in both sexes. Merckx, Kaiser and Van Dyck (2018) demonstrate increasing body size in macro-moths due to increasing habitat fragmentation in urban areas. Thus, over the 137 years covered in our study, increasingly fragmented habitats due to urbanisation in Berlin Antrop (2000), and intensified agriculture in Brandenburg (Cochrane & Jonas, 1999), could have opposed the potential effects of ALAN. Interestingly, it has been shown that attraction radii of streetlights overlap in most cases, building barriers for moths (Degen et al., 2016). Therefore, ALAN might have increased the fragmentation of nocturnal habitats, also in our study area, limiting moth dispersal, and thus, indirectly inducing changes in body size but not in relative forewing length.

Our results revealed that trait and sex-depended changes in *A. exclamationis* over the past 137 years in the Berlin-Brandenburg region took place. However, these changes could not be directly linked to increasing ALAN. Nevertheless, we assume trait changes to have been indirectly induced by ALAN as a result of habitat fragmentation (Degen et al., 2016) and females' changed perception of host-plants (Callahan, 1957). However, we found a trend of sex-dependant changes in eye size which may be directly related to different levels of light pollution, and thus a first sign of light pollution driving morphological trait change.

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Declaration of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.05.004.

References

Altermatt, F., & Ebert, D. (2016). Reduced flight-to-light behavior of moth populations exposed to long-term urban light pollution. *Biology Letters*, *12*, 20160111 https://dx.doi.org/10.1098/rsbl.2016.0111.

Antrop, M. (2000). Changing patterns in the urbanized countryside of western Europe. *Landscape Ecology*, *15*, 257–270. doi:10.1023/A:1008151109252.

Baker, R. R., & Sadovy, Y. (1978). The distance and nature of light-trap response of moths. *Nature*, *276*, 818–821. doi:10.1038/276818a0.

Beall, G., & Williams, C. B. (1945). Geographic variation in the wing length of *Danaus plexippus* (Lep. Rhopalocera). In *Proceedings of the royal entomological society of London* (pp. 65−76). doi:10.1111/j.1365-3032.1945.tb01068.x.

Bernays, E. A. (2001). Neural limitations in phytophagous insects: Implications for diet breadt and evolution of host affiliation. *Annual Reviews of Entomology*, *46*, 703–727. doi:10.1146/annurev.ento.46.1.703.

Bernays, E. A., & Wcislo, W. T. (1994). Sensory capabilities, information-processing, and resource specialization. *The Quarterly Review of Biology*, *69*, 187–204. doi:10.1086/418539.

Callahan, S. P. (1957). Oviposition response of the imago of the Corn Earworm *Heliothis zea* (Boddie), to various wave lengths of light. *Annals of the Entomological Society of America*, *50*, 444–452. doi:10.1093/aesa/50.5.444.

Chai, P., & Srygley, R. B. (1990). Predation and the flight, morphology, and temperature of neotropical rain-forest butterflies. *The American Naturalist*, *135*, 748–765. doi:10.1086/285072.

Cochrane, A., & Jonas, A. (1999). Reimagining Berlin: World city, national capital or ordinary place? *European Urban and Regional Studies*, *6*, 145–164 https://doi.org/10.1177%2F096977649900600204.

Conrad, F. K., Warren, S. M., Fox, R., Parsons, S. M., & Woiwod, P. I. (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, *132*, 279–291. doi:10.1016/j.biocon.2006.04.020.

Dall, S. R. X., & Cuthill, I. C. (1997). The information costs of generalism. *Oikos (Copenhagen, Denmark)*, *80*, 197–202. doi:10.2307/3546535.

Degen, T., Mitesser, O., Perkin, K. E., Weiß, N.-S., Oehlert, M., Matting, E., et al. (2016). Street lighting: Sex-independent impacts on moth movement. *Journal of Animal Ecology*, *85*, 1352–1360. doi:10.1111/1365-2656.12540.

Doudna, J. W., & Danielson, B. J. (2015). Rapid morphological change in the masticatory structures of an important ecosystem service provider. *PloS ONE*, *10*, e0127218. doi:10.1371/journal.pone.0127218.

Ebert, G., Rennwald, E., & Bartsch, D. (1997). *Die Schmetterlinge Baden-Württembergs. Band 5 - Nachtfalter III*. Stuttgart: Ulmer Verlag.

In Eisenbeis, G. (2006). Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. (Eds.), In C. Rich, & T. Longcore (Eds.), *Ecological consequences of artificial night lighting* In. (pp. 281−304). Washington: Island Press (pp..

Eisenbeis, G., & Hänel, A. (2009). Light pollution and the impact of artificial night lighting on insects. (Eds.), In M. J. McDonnell, A. H. Hahs, J. H. Breuste (Eds.), *Ecology of cities and towns* (Eds.). (pp. 243−263). Cambridge: Cambridge University Press.

Fayle, M. T., Sharp, E. R., & Majerus, N. E. M. (2007). The effect of moth trap type on catch size and composition in British Lepidoptera. *British Journal of Entomology and Natural History*, *20*, 221–232.

Fox, J., Weisberg, S., & Price, B. (2019). *An R companion to applied regression* (3rd edition). https://cran.r-project.org/package=carData.

Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013). The ecological impacts of night-time light pollution: A mechanistic appraisal. *Biological Reviews*, *88*, 912–927. doi:10.1111/brv.12036.

Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). Reducing the ecological consequences of night-time light pollution: Options and developments. *Journal of Applied Ecology*, *49*, 1256–1266 https://doi: 10.1111/j.1365-2664.2012.02212.x.

Gaston, K. J., Visser, M. E., & Hölker, F. (2015). The biological impacts of artificial light at night: The research challenge. *Philosophical Transactions of the Royal Society B*, *370*, 20140133. doi:10.1098/rstb.2014.0133.

Grant, G. G. (1987). Copulatory behaviour of spruce budworm, *Choristoneura funiferana* (Lepidoptera: Tortricidae): Experimental analysis of the role of sex pheromone and associated stimuli. *Annals of the Entomological Society of America*, *80*, 78–88. doi:10.1093/aesa/80.1.78.

Hallmann, A. C., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., et al. (2017). More than 75 percent decline over 27 years in total flying insects' biomass in protected areas. *PLoS ONE*, *12*, e0185809. doi:10.1371/journal.pone.0185809.

Haubner, F. (1962). Aus den Anfängen der Öffentlichen Elektrizitätsversorgung Berlin (1882-1899). *Zeitschrift für Firmengeschichte und Unternehmerbiographie*, *1*, 1–11. doi:10.1515/zug-1962-0102.

Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., et al. (2010a). The dark side of light: A transdisciplinary research agenda for light pollution policy. *Ecology and Society*, *15* Art. 4. https://www.jstor.org/stable/26268230.

Hölker, F., Wolter, C., Perkin, E. K., & Tockner, K. (2010b). Light pollution as a biodiversity threat. *Trends in Ecology and Evolution*, *25*, 681–682 https://dx.doi.org/10.1016/j.tree.2010.09.007.

Hopkins, R. G., Gaston, J. K., Visser, E. M., Elgar, A. M., & Jones, M. T. (2018). Artificial light at night as a driver of evolution across urban-rural landscapes. *Frontiers in Ecology and the Environment*, *16*, 472–479. doi:10.1002/fee.1828.

Johnson, L., Mantle, L. B., Gardner, L. J., & Backwell, R. Y. P. (2013). Morphometric measurements of dragonfly wings: The accuracy of pinned, scanned and detached measurement methods. *ZooKeys*, *276*, 77–84. doi:10.3897/zookeys.276.4207.

Jones, C. B. H., Lim, S. K., Bell, R. J., Hill, K. J., & Chapman, W. J. (2016). Quantifying interspecific variation in dispersal ability of noctuid moths using an advanced tethered flight technique. *Ecology and Evolution*, *6*, 181–190. doi:10.1002/ece3.1861.

Kavanaugh, D. H. (1979). Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebrza* species and subspecies. *Proceedings of the California Academy of Science*, *42*, 87–133.

Keinath, S., Frisch, J., Müller, J., Mayer, F., & Rödel, M.-O. (2020). Spatio-temporal color differences between urban and rural populations of a ground beetle during the last 100 years. *Frontiers in Ecology and Evolution - Urban Ecology*, *7*. doi:10.3389/fevo.2019.00525 Art. 525.

Kuechly, H. U., Kyba, C. C., Ruhtz, T., Lindemann, C., Wolter, C., Fischer, J., et al. (2012). Aerial survey and spatial analysis of sources of light pollution in Berlin, Germany. *Remote Sensing of Environment*, *126*, 39–50. doi:10.1016/j.rse.2012.08.008.

Kyba, C. C. M., Garz, S., Kuechly, H., De Miguel, A. S., Zamorano, J., Fischer, J., et al. (2015). High-resolution imagery of earth at night: New sources, opportunities and challenges. *Remote Sensing*, *7*, 1–23. doi:10.3390/rs70100001.

Kyba, C. C. M., Kuester, T., & Kuechly, U. H. (2017a). Changes in outdoor lighting in Germany from 2012 to 2016. *International Journal of Sustainable Lighting*, *19*, 112–123. doi:10.26607/ijsl.v19i2.79.

Kyba, C. C. M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., et al. (2017b). Artificially lit surface of Earth at night increasing in radiance and extent. *Science Advances*, *3*, e1701528. doi:10.1126/sciadv.1701528.

Levins, R., & MacArthur, R. (1969). An hypothesis to explain the incidence of monophagy. *Ecology*, *50*, 910–911. doi:10.2307/1933709.

Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, *2*, 191–198. doi:10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2.

Merckx, T., Kaiser, A., & Van Dyck, H. (2018). Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Global Change Biolology*, *24*, 3837–3848. doi:10.1111/gcb.14151.

Light pollution map (2019). Interactive world light pollution map. www.lightpollutionmap.info. Accessed 06 Mai 2020.

Miller, D.S., Straka, W., Mills, P.S., Elvidge, D.C., Lee, F.T., Solbrig, J. et al. (2013). Illuminating the capabilities of the Suomi natural Polar-Orbiting Partnership (NPP) Visible Infrared Radiometer Suite (VIIRS) day/night band. *Remote Sensing*, 5, 6717−6766. https://doi.org/10.3390/rs5126717

Navara, K. J., & Nelson, J. R. (2007). The dark side of light at night: Physiological, epidemiological, and ecological consequences. *Journal of Pineal Research*, *43*, 215–224. doi:10.1111/j.1600-079X.2007.00473.x.

Niemeier, S., Müller, J., Struck, U., & Rödel, M.-O. (2020). Superfrogs in the city: 150 year impact of urbanization and agriculture on the European Common Frog. *Global Change Biology*, *26*, 6729–6741 https//doi.org/10.1111/gcb.15337.

Nieminen, M., Rita, H., & Uuvana, P. (1999). Body size and migration rate in moths. *Ecography*, *22*, 697–707. doi:10.1111/j.1600-0587.1999.tb00519.x.

Owens, C. S. A., Cochard, P., Durrant, J., Farnworth, B., Perkin, K. E., & Seymoure, B. (2020). Light pollution is a driver of insect decline. *Biological Conservation*, *241*, 108259. doi:10.1016/j.biocon.2019.108259.

R Core Team. (2020). *R: A language and environment statistical computing*. Vienna: R Foundation for Statistical Computing URL https://www.R-project.org/.

Ribbe, W., Bohm, E., Schich, W., & Schulz, K. (2002a). Geschichte berlins. *Band 1: Von der frühgeschichte bis zur industrialisierung*. München: Beck.

Ribbe, W., Bohm, E., Schich, W., & Schulz, K. (2002b). Geschichte berlins. *Band 2: Von der märzrevolution bis zur gegenwart*. München: Beck.

Rich, C., & Longcore, T. (2006). *Ecological consequences of artificial night lighting*. Washington: Island Press.

Rutowski, R. L., Gislén, L., & Warrant, E. J. (2009). Visual acuity and sensitivity increase allometrically with body size in butterflies. *Arthropod Structure and Development:* (pp. 91−100)*38*. doi:10.1016/j.asd.2008.08.003.

Scoble, M. J. (1992). *The Lepidoptera: Form, function and diversity*. Oxford, UK: Oxford University Press.

Slade, E. M., Merckx, T., Riutta, T., Bebber, D. P., Redhead, D., Riordan, P., et al. (2013). Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology*, *94*, 1519–1530. doi:10.1890/12-1366.1.

Somers-Yeates, R., Hodgson, D., McGregor, P. K., Spalding, A., & Ffrench-Constant, R. (2013). Shedding light on moths: Shorter wavelengths attract noctuids more than geometrids. *Biology Letters*, *9*, 20130376. doi:10.1098/rsbl.2013.0376.

Sukopp, H., & Werner, P. (1983). Urban environments and vegetation. (Eds.), In W. Holzner, M. J. A. Werger, I. Ikusima (Eds.), *Man's impact on vegetation* (Eds.). The Hague: Dr. W. Junk Publishers.

Sutton, P. C. A. (2003). A scale adjusted measure of 'urban sprawl' using nighttime satellite imagery. *Remote Sensing of Environment*, *86*, 353–369. doi:10.1016/S0034-4257(03)00078-6.

Tóth, M., Szarukán, I., Dorogi, B., Gulyás, A., Nagy, P., & Rozgonyi, Z. (2010). Male and female Noctuid Moths attracted to synthetic lures in Europe. *Journal of Chemical Ecology*, *36*, 592–598. doi:10.1007/s10886-010-9789-z.

United Nations (2002). *World population prospects: The 2001 revision*. Population division of the department of economic and social affairs of the United Nations Secretariat.

Van Langevelde, F., Ettema, A. J., Donners, M., WallisDeVries, F. M., & Groenendijk, D. (2011). Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, *144*, 2274–2281. doi:10.1016/j.biocon.2011.06.004.

Van't Hof, A., Edmonds, E., Dalikova, M., Marec, F., & Saccheri, J. I. (2011). Industrial melanism in British Peppered Moths has a singular and recent mutational origin. *Science (New York, N.Y.)*, *332*, 958–960. doi:10.1126/science.1203043.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with s* (4th ed.). New York: Springer-Verlag https://www.stats.ox.ac.uk/pub/MASS4.

Wehner, R. (1984). Astronavigation in insects. *Annual Review of Entomology*, *29*, 277–298 https://doi.org/10.1146/annurev.en.29.010184.001425.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York: Springer-Verlag.

Williams, C. B. (1939). An analysis of four years captures of insects in a light trap. Part 1. General survey; sex proportion; phenology; and time of flight. *Transactions of the Royal Entomological Society of London*, *89*, 79–132.

Xu, J., Liu, N., & Zhang, R. (2013). Major potato pests in China. (Eds.), In P. Giordanengo, C. Vincent, A. Alyokhin (Eds.), *Insect pests of potatos − Global perspectives on biology and management* (Eds.). New York: Elsevier.

Yack, J. E., Johnson, S. E., Brown, S. G., & Warrant, E. J. (2007). The eyes of *Macrosoma* sp. (Lepidoptera: Hedyloidea): A nocturnal butterfly with superposition optics. *Arthropod Structure and Development*, *36*, 11–22. doi:10.1016/j.asd.2006.07.001.

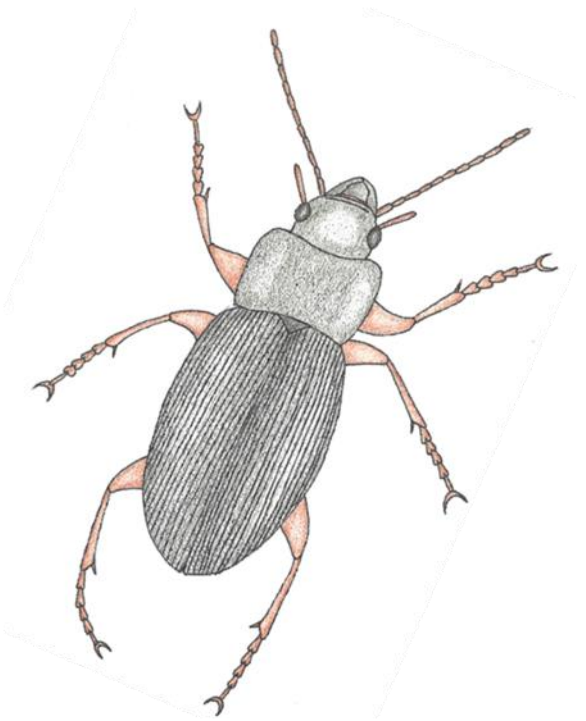
Yagi, N., & Koyama, N. (1963). *The compound eye of lepidoptera: Approach from organic evolution*. Tokyo: Shinkyo Press.

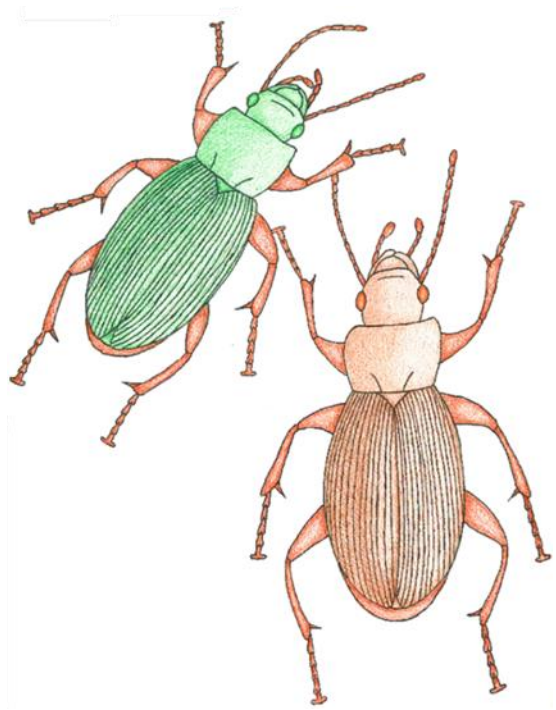
Zerbe, S., Maurer, U., Schmitz, S., & Sukopp, H. (2002). Biodiversity in Berlin and its potential for nature conservation. *Landscape and Urban Planning*, *62*, 139–148. doi:10.1016/S0169-2046(02)00145-7.

5.2 Paper 2

Body sizes and dietary niche of two ground beetle species from urban and rural populations, tracked from 1900 to today

Keinath, S., Frisch, J., Müller, J., Mayer, F., Struck, U., & Rödel, M.-O. *Body sizes and dietary niche of two ground beetle species from urban and rural populations, tracked from 1900 to today.*





Body sizes and dietary niche of two ground beetle species from urban and rural populations, tracked from 1900 to today

Silvia Keinath[1;2], Johannes Frisch[1], Johannes Müller[1;2], Frieder Mayer[1;2], Ulrich Struck[1;3], Mark-Oliver Rödel[1;2]

Increasing urbanisation and intensified agriculture lead to rapid transitions of ecosystems. Species persisting in changing environments may respond to these changes, for instance by altering morphology and biochemistry across space and/or time. Respective long-term data may be extracted from museum collections, combined with recent samples, covering areas with documented environmental changes. In our study we tested whether rural and urban populations of two ground beetle species, *Harpalus affinis* and *H. rufipes*, exhibit spatio-temporal intraspecific differences in body size and signatures of nitrogen and carbon stable isotopes in different tissues. We examined beetles, collected from the early 20th century until today, in the Berlin-Brandenburg region, Germany, a region with increasing levels of urbanisation and intensified agriculture throughout the last century. Our results revealed no spatio-temporal changes in body size in both species' females. Body size of *H. rufipes* males decreased in the city whereas they remained constant in rural areas over time. We discuss whether our findings might be due to increasing urban heat or differences in activity pattern. Although nitrogen isotope ratios were mostly higher in species' tissues from agricultural habitats, some reached the same enrichment in urban habitats. We assume that highly urbanised habitats exhibit similar nitrogen isotope ratios than agricultural ones. The carbon isotopic signatures did not differ in species between habitats, indicating no different energy bases. Our results show that increasing urbanisation and intensified agriculture are influencing species' morphology and biochemistry. However, changes in morphology are species and sex specific.

Keywords: Carbon; *Harpalus affinis*; *Harpalus rufipes*; Nitrogen; Spatio-temporal gradient; Stable isotopes.

Introduction

Human land-use, mostly for settlements and agriculture, is globally increasing (Bairoch and Goertz 1986; Antrop 2004). These changes lead to rapid transitions from natural to altered ecosystems (Hobbs et al. 2013; Jeltsch et al. 2013), which differ from natural systems in species compositions and/or functions, and are thus defined as novel ecosystems (Harris et al. 2006; Root and Schneider 2006; Ricciardi 2007). As a consequence of environmental changes, many native species disappear whereas non-native species may establish in novel ecosystems (Kenis et al. 2009; Ziegler 2011). However, some species persist during and beyond the transition process (van´t Hof et al. 2011; Doudna and Danielson 2015), because they are able to cope with or adapt to new conditions (Cook and Saccheri 2013; Giraudeau et al. 2014). Unfortunately, in most cases it is not clear

[1] Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin, Germany [2] Berlin-Brandenburg Institute of Advanced Biodiversity Research – BBIB, Königin-Luise-Str. 2-4, 14195 Berlin, Germany [3] Department of Earth Science, Freie Universität, Berlin, Malteserstr. 74-100, 12249 Berlin, Germany

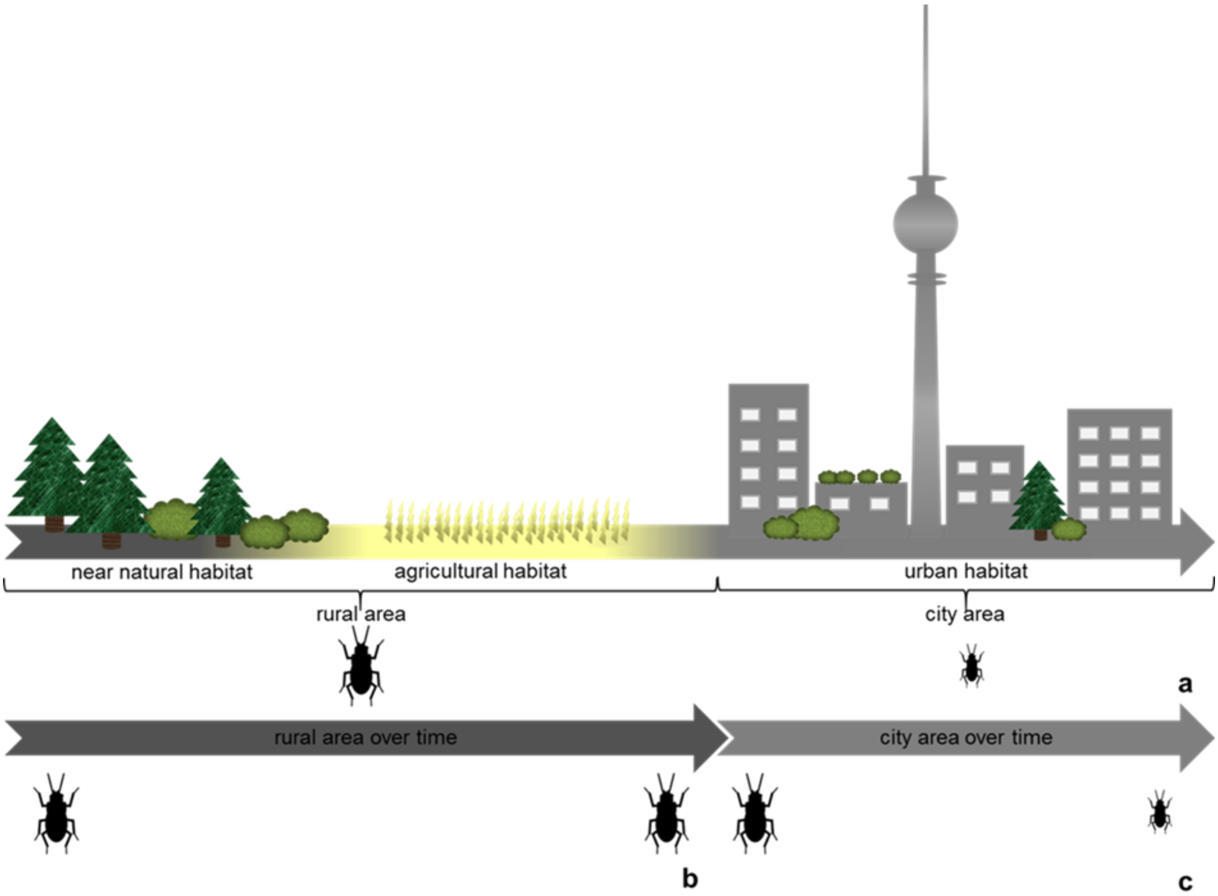


Figure 1 Hypothetic anthropogenic influence on body size of ground beetles, in space and time. Along a land-use gradient we expected to find smaller sized beetles in urban habitats compared to agricultural habitats (a). Whereas we expected no differences in body sizes over time in rural areas (composed of near natural and agricultural habitats) (b), beetles were expected to shrink in the city over time (c).

which traits enable species to persist (Palkovacs et al. 2011). Direct observations of behavioural, physiological or morphological trait change are usually difficult or impossible to get, due to extended time periods during which changes take place. However, this challenge might be bypassed by investigating preserved specimens in museum collections, using morphological traits as proxies for species' ecological and physiological modifications (Rocha et al. 2014). These datasets might be complemented with recent samples to cover spatio-temporal gradients (van´t Hof et al. 2011; Doudna and Danielson 2015; Keinath et al. 2020; Niemeier et al. 2020). A useful morphological trait, indicating habitat quality, is body size (Niemelae et al. 2002; Kotze and O´Hara 2003). Ectothermic animals, such as insects, may be impacted by environmental change to a larger extend than endotherms, because their development is directly depending on environmental temperatures. Higher temperatures may lead to faster larval development, earlier start of metamorphosis, resulting in smaller sized imagines (Atkinson 1994; Kingsolver and Huey 2008). Because cities are often displaying higher temperatures, so called urban heat islands, than their rural surroundings (Oke 1973), living in the city may lead to smaller sized insects (Kotze et al. 2011; Brans et al. 2017) (Fig. 1).

Apart from morphological traits, biochemistry, i.e. stable isotope compositions, reflect the living conditions of an individual (Peterson and Fry 1987). For instance, in plants and animals, carbon and nitrogen are each present with two stable isotopes, $^{13}C/^{12}C$, and $^{15}N/^{14}N$, respectively (Rosing et al. 1998). Whereas carbon isotope signatures provide information about the respective energy base of an animal's diet (DeNiro and Epstein 1978; Ponsard and Arditi 2000; Gratton and Forbes 2006), i.e. the proportion of C3 and C4 plants in the respective environments (Degens 1969; Schwarcz 1969), the nitrogen isotope composition provides information about the position of this individual in the food web (Birkhofer et al. 2011). In intensively managed agricultural landscapes, the application of chemical and biological nitrogen bearing fertilizers may also influence nitrogen isotopic composition (Freyer and Aly 1974; Shearer et al. 1974; DeNiro and Epstein 1980; Jenkinson 2001). Thus, different $^{15}N/^{14}N$ ratio may indicate differences between intensively managed agricultural landscapes and less impacted habitats (Birkhofer et al. 2011). The composition of stable isotopes might also differ in different body parts and tissue types. Depending on the turnover time of different tissue types, it is possible to determine both, long-term and short-term dietary preferences. The isotopic signature of slow turnover tissues, like chitin of holometabolic insects, are described to represent the nutritive status of the larval stage, whereas tissues that turnover faster, like muscles, represent the dietary conditions of adults (Peterson and Fry 1987; Gratton and Forbes 2006). Thus, analyses of stable isotopes from different tissues provide information if different stages of a species exploit different nutrient sources in different habitats, and may even reflect specimens' dispersal from one into another habitat (Hood-Nowotny and Knols 2007; Schallhart et al. 2009).

Among holometabolic insects, carabid beetles are often used to track environmental change (Thiele 1977; Sota et al. 2000) such as urbanisation (Sustek 1992; Weller and Ganzhorn 2003). For our study, we selected two carabid species, *Harpalus affinis* and *H. rufipes* that are common in the German Berlin-Brandenburg region and are well-represented in the collection of the Museum für Naturkunde, Berlin, covering the past 125 years.

We hypothesize on the temporal scale that both species' specimens are smaller in the city today than in the past (Fig. 1). On the spatial scale we hypothesize specimens of both species to be smaller in the city in comparison to rural specimens. Both predictions are based on the presumed response of developing beetles to urban heat islands (Kotze et al. 2011; Brans et al. 2017). Furthermore, we hypothesize body size to remain constant over time in both species when occurring in rural areas due to none or little temperature differences in these habitats through time (Oke 1973) (Fig. 1).

We further hypothesize that higher enrichment of the heavy nitrogen isotopes in beetles occurring in agricultural in comparison to urban habitats reflect the use of fertilizers (Birkhofer et al. 2011). Stable carbon isotope composition is further predicted to differ between beetles occurring in agricultural and urban habitats as a consequence of different plant compositions (DeNiro and Epstein 1978; Ponsard and Arditi 2000). Further, we hypothesize to observe intraspecific differences of isotopic signatures in different tissues of the beetles (Peterson and Fry 1987; Gratton and Forbes 2006) if adult beetles dispersed from larval habitats into another habitat type (Hood-Nowotny and Knols 2007; Schallhart et al. 2009).

Material and Methods

Study region

In the German Berlin-Brandenburg region, rapid environmental transitions occurred during the last century (Cochrane and Jonas 1999). The city of Berlin is a fast-growing metropolis, whose population density increased during the 19th and 20th centuries, with a decline during both World Wars. The destruction of the city was followed by a phase of rapid reconstruction in the direct aftermath of the Second World War (Kratke 2000), leading to a high level of urbanization today (Antrop 2000). Brandenburg, the German federal state surrounding Berlin, mostly consists of rural areas comprising near natural environments, as well as intensively used agricultural monocultures (Cochrane and Jonas 1999).

Study species

The ground beetle (Coleoptera, Carabidae) *Harpalus affinis* is widespread in Europe (Wrase 2004). It is a medium-sized (8.5-12 mm), diurnal generalist of open habitats, predominantly feeding on weed seeds and occasionally on insect larvae (Townsend 1992; Sunderland et al. 1995) with variable metallic colouration (Wrase 2004; Keinath et al. 2020). Adults are winged and volant, are spring breeders, and active between March and October, with the main activity period between May and June (Townsend 1992; Trautner 2017).

Harpalus rufipes is widespread in the Palaearctic, medium sized (11-16 mm), predominantly nocturnal (Wrase 2004), and attracted by artificial light sources (Kegel 1990; Szentkirályi et al. 2003). Adults are generalists in deforested habitats and tend to be granivorous (Bažok et al. 2007; Trautner 2017). Larvae are omnivorous (Toft and Bilde 2002). It is a summer breeder and active between April and October, with a maximum between July and August (Trautner 2017).

Both species are eurytopic and encountered in open environments across a wide range of different habitats from arable fields (Sunderland et al. 1995; Harrison and Gallandt 2012), vineyards, grasslands (Trautner 2017); semi-natural (Anjum-Zubair et al. 2015) and less human impacted, near natural landscapes (Townsend 1992; Holec et al. 2006) to urban green spaces (Deichsel 2006). In both species, males differ from females by wider tarsi of the pro- and mesothoracal legs (Lindorth 1945; Townsend 1992).

In total we examined 624 *H. affinis* (382 males; 242 females), thereof 562 museum vouchers, collected between 1893 and 1998, and 62 recently collected specimens. In total, 300 beetles were from Berlin and 324 from Brandenburg.

We also examined in total 180 *H. rufipes* (97 males; 83 females), thereof 86 museum vouchers, spanning the years 1892 to 1994, and 94 recently collected specimens, 62 beetles were from Berlin and 118 from Brandenburg.

Museum vouchers of both species from Berlin with available habitat information have been collected at roadsides, parks, dumpsites, garden plots, and ruderal sites. Vouchers from Brandenburg have been collected at meadows, forest edges, and arable landscapes.

Recent specimens from Berlin of both species have been sampled at eight urban dry grassland sites in June and July 2017. Respective specimens from Brandenburg originated from agricultural winter wheat and soy fields, as well as from fallow grass stripes in between fields. They were collected in the administrative districts Nordwestuckermark from May to June 2016, in the Uckermark in June 2017, and from May to July 2017 in Märkisch-Oderland. Recently sampled beetles were caught with pitfalls. All specimens are deposited in the collection of the Museum für Naturkunde, Berlin (Tab. B & C in supplementary material).

Body length measurements

Body length was measured with the aid of a dissecting microscope and a measuring ocular (Leica MS5), using a revolving table placed under the microscope to enable planar measurements of the pinned beetles. Standardized Body Length (SBL) measurements, following Kavanaugh (1979), comprised head length (distance from labium to vertex behind eyes), pronotal (maximal distance from anterior to posterior margin) and elytral length (sutural length; distance from anterior margin of the scutellum to posterior end of the elytra). Measurement errors (*H. affinis*: ± 0.06 mm; *H. rufipes*: ± 0.09 mm) were determined by the mean accuracy of repeated measurements of a randomized chosen subset of 10 specimens per species. All measurements were taken by one person (SK) without prior knowledge of sex, region of origin, and habitat of the respective specimens (Tab. B & C in supplementary material).

Stable nitrogen and carbon isotopic composition

For stable nitrogen and carbon isotope analyses, we selected 20 recently collected specimens of each species. We examined 10 specimens (5 males and 5 females) of *H. affinis* from nine dry grassland sites in Berlin, and the same number of specimens of *H. rufipes* from seven dry grassland sites in Berlin. Furthermore, we examined 10 specimens of each species (each 5 males and 5 females) from agricultural winter wheat fields and adjacent green strips from the Nordwest Uckermark (Tab. D1-6 in supplementary material).

From all individuals we removed and weighted one milligram of each legs, cuticula, and thorax muscle tissues. The samples were dried in an oven at 40°C for 12 hours. Stable isotope analysis and concentration measurements of nitrogen and carbon of the respective samples were performed simultaneously with a THERMO Fisher Scientific Delta V isotope ratio mass spectrometer, coupled to a THERMO Flash EA 1112 elemental analyser via a THERMO Conflo IV-interface, in the stable isotope laboratory of the Museum für Naturkunde, Berlin. Stable isotope ratios are expressed in the conventional delta notation ($\delta^{13}C$ / $\delta^{15}N$) relative to atmospheric nitrogen (Mariotti 1983) and VPDB (Vienna PeeDee Belemnite standard). Standard deviation for repeated measurements of lab standard material (peptone) was generally better than 0.15‰ for nitrogen and carbon, respectively. Standard deviations of concentration measurements of replicates of our lab standard were <3% of the concentration analyzed. From the *H. affinis* muscle samples, seven (2 agricultural; 5 urban individuals) comprised not enough material for analyses and were excluded.

Data classification

All beetles were classified by species, sex and origin. For body size analyses beetles with origin in Berlin were classified as coming from a ‘city area’, Brandenburg specimens were classified as coming from a 'rural area'. Beetles with body size data were partly connected to further, more detailed, habitat information (e.g. ruderal sites, dumpsites, edges of streets, parks, and agricultural habitats). Respective individuals were used for in depth habitat comparisons between 'urban habitats' and 'agricultural habitats'. It is suspected that old museum specimens of both species collected in the 19th century without any further sampling information except 'Berlin' on their labels were sampled at the periphery of Berlin. However, we assigned them to the category 'city area' because we assume already higher levels of urbanisation at the periphery of Berlin compared to its rural surroundings as described by Reif (2003).

For temporal comparisons beetles classified in 'city area' and 'rural area' were used. Beetles of each category were assigned to one of three distinct time periods: 1892-1949, 1957-1998 and 2016-2017. Time period classification was based on a combination of practical reasons (availability of sufficient numbers of beetles) and the history of urbanization and agricultural techniques in our study region (see Keinath et al. 2020).

During the first time period (1892-1949), the Berlin-Brandenburg region was mainly impacted by the effects of the industrial revolution and First and Second World Wars (Ribbe et al. 2002a, b). Furthermore, Berlin expanded to "Groß-Berlin" in the 1920´s, resulting in rapid construction of buildings and streets (Buesch and Haus 1987). Then, the Berlin population was larger than ever (Ribbe et al. 2002b). Industrialisation and application of chemical fertilizer in intensified agriculture led to a first high level of environmental pollution (Pamme 2003; Erisman et al. 2008). During the second time period (1957-1998), the reconstruction of Berlin was finalized, the human population was, however, much below the pre-war conditions (Schildt and Sywotlek 1993, Ribbe et al. 2002b). By the end of the 1950s, first ideas of environmental protection became implemented politically (Pamme 2003), resulting in efforts to reduce the environmental pollution of the city (UNEP/WHO 1993; UBA 1998) and the application of chemical fertilizer in agriculture (Tilman et al. 2002; Erisman et al. 2008). Therefore, we treat this time period as an intermediate stage of environmental pollution. From 1999 to today the Berlin population continuously increased (United Nations 2018), and environmental protections became politically established (Pamme 2003). Whereas numerous museum specimens were available from the first two time periods, only few specimens were available from the most recent period. We therefore complemented the museum specimens by own samples (2016-2017) (Tab. B & C in supplementary material).

Statistical analyses

We used the R-Project, version 3.4.0 (R Core Team 2017) for all analyses. For visualisation of the results, we draw boxplots with the R-package ggplot2 (Wickham 2016). For testing for normal distribution, we used Shapiro Wilk test. In further analyses we used the non-parametrical Wilcoxon Rank Sum test for comparing Standardized Body Lengths (SBL) between sexes (females, males) 'SBL~Sex'; areas (rural, city) 'SBL~Area', and habitats, (urban, agricultural) 'SBL~Habitat'. For comparing SBL between the three time periods (1892-1949; 1957-1998; 2016-2017) for each area (rural, city), we used the non-parametrical Kruskal-Wallis rank sum test, ‘SBL~Time Period’, and Dunn-test for single comparisons between the respective time periods with Bonferroni correction for multiple testing (dunn.test: Dinno 2017; FSA: Ogle et al. 2019). We further used Levene’s Test for testing variation of SBL between habitats, areas and time periods, the latter by using Bonferroni correction for multiple testing.

For stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes comparisons of different tissues (cuticula, legs, thoracic muscles), between sexes ‘$\delta^{15}N$~Sex’; ‘$\delta^{13}C$~Sex’ and between agricultural and urban habitats ‘$\delta^{15}N$~Habitat’; ‘$\delta^{13}C$~Habitat’ we used the non-parametrical Wilcoxon Rank Sum test. For comparing $\delta^{15}N$ and $\delta^{13}C$ isotopic enrichments between tissues either of agricultural or urban habitats ‘$\delta^{15}N$~Tissue’; ‘$\delta^{13}C$~Tissue’, we applied the Kruskal-Wallis Rank Sum tests. We further used Levene’s Test for testing variation of stable nitrogen and carbon isotopes of the different tissues within the respective habitat and species.

Results

For body size and stable isotopes, we tested differences of medians to examine trait changes in space and time. We further tested variabilities to make assertions about traits’ consistence.

Body size

When testing medians, females were significantly larger than males in both species (Wilcoxon rank sum test: *H. affinis*: N = 624; p < 0.001; *H. rufipes*: N = 178; p < 0.001) (Tab. A1). Both species did not differ in their body size in both sexes between agricultural and urban habitats and between rural and city areas (Tab. A1; Fig. 2 & 3a, b). Likewise, body lengths of females in both species remained constant through the three time periods, both in rural and city areas (Tab. A1; Fig. 2c & 3c). This was also the case for male *H. affinis* (Tab. A1; Fig. 2c) from rural habitats.

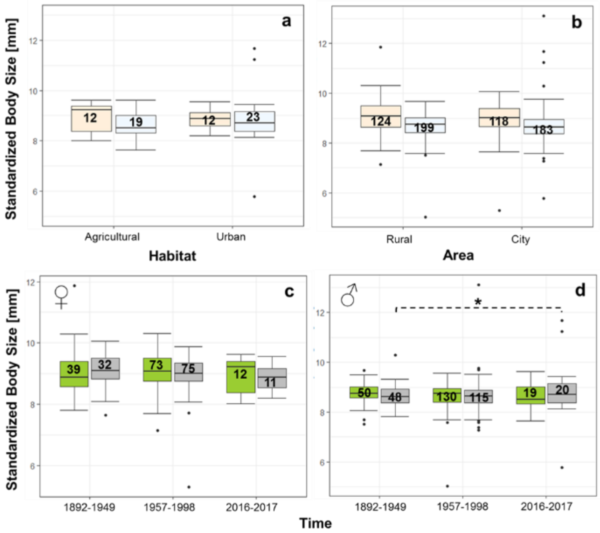


Figure 2 Body lengths of *Harpalus affinis* from agricultural and urban habitats (a) and rural and city areas (b) of females (pink boxes) and males (blue boxes); females (c) and males (d) in rural (green boxes) and city (grey boxes) areas over time. Numbers within boxes indicate sample sizes, dotted brackets with stars indicate significant differences in variability of body size (* = p < 0.05).

In city areas, however, body lengths of *H. rufipes* males changed through time (Kruskal-Wallis rank sum test; n = 41; p < 0.01) (Tab. A1; Fig. 3d). Male *H. rufipes* were equally large in 1892-1949 and 1957-1998 (Kruskal-Wallis Dunn-Test; n = 29; Z = -0.934; p unadjusted = 0.350; p = 1), but in 2016-2017 males were significantly smaller (1957-1998; Kruskal-Wallis Dunn-Test; n = 20; z = 2.620; p unadjusted = 0.009; p = 0.026; 1892-1949: Kruskal-Wallis Dunn-Test, n = 31; z = 3.022; p unadjusted = 0.003; p = 0.008).

When testing the variability of body size of each sex per species between habitats, areas and areas over time, no differences in females of both species and males of *H. affinis* between agricultural and urban habitats were found (Tab. A2). However, in *H. rufipes* males the variability of body sizes was significantly higher in urban compared to agricultural habitats (Levene's test: n = 45; df = 43; F = 5.391; p = 0.025; Tab. A2; Fig. 3a), and also significantly higher in city areas in comparison to rural areas (Levene's test: n = 96; df = 94; F = 5.157; p = 0.025; Tab. A2; Fig. 3b).

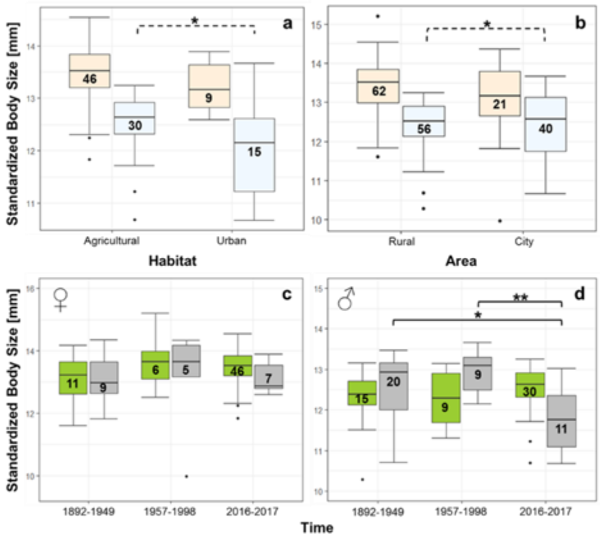


Figure 3 Body lengths of *Harpalus rufipes* from agricultural and urban habitats (a) and rural and city areas (b) of females (pink boxes) and males (blue boxes); females (c) and males (d) in rural (green boxes) and city (grey boxes) areas over time. Numbers within boxes indicate sample sizes, dotted brackets with stars indicate significant differences in variability of body size, drawn through brackets with stars indicate significant differences in body size (* = p < 0.05; ** = p < 0.01).

The variability of body size in both species' sexes did not differ in rural areas over time, as well as in both species' females and *H. rufipes* males in city areas over time. However, in *H. affinis* males the variability differed between time periods (Levene's test; n = 68; df = 180; F = 0.281; p = 0.020; Tab. A2; Fig. 2d). The variability of male size in *H. affinis* was equally high in 1892-1949 and 1957-1998 (Levene's test with Bonferroni correction; n = 163; p unadjusted = 0.366; p = 1) as well as between 1957-1998 and 2016-2017 (Levene's test with Bonferroni correction; n = 135; p unadjusted = 0.026; p = 0.079), but in 2016-2017 variability significantly increased compared to 1892-1949 (Levene's test with Bonferroni correction; n = 68; p unadjusted = 0.013; p = 0.038) (Fig. 2d).

Stable Isotopes

The stable nitrogen and carbon isotope composition within particular tissues of both species did not differ significantly between sexes (Tab. A3). For subsequent analyses we thus pooled the data of males and females of each species. Compared to urban habitats, $\delta^{15}N$ was significantly higher in cuticula and legs of *H. affinis* from agricultural habitats (Wilcoxon rank sum test: cuticula: n = 10, p ≤ 0.01; legs: n = 10; p ≤ 0.01) (Tab. A3; Fig. 4b). The nitrogen isotope signature of *H. affinis* muscles did not significantly differ between habitats (Tab. A3; Fig. 4b). Similarly, carbon isotope signatures from different tissues of *H. affinis* did not differ between agricultural and urban habitats (Tab. A3; Fig. 4d). In *H. rufipes*, ^{15}N was significantly enriched in cuticula, legs and muscles in beetles originating from agricultural habitats (Wilcoxon rank sum test: cuticula: n = 10, p > 0.05; legs: n = 10; p > 0.05; muscles: n = 10, p > 0.01) (Tab. A3; Fig. 4a). Stable carbon isotope signatures of *H. rufipes* tissues did not differ between beetles from urban and agricultural habitats (Tab. A3; Fig. 4c).

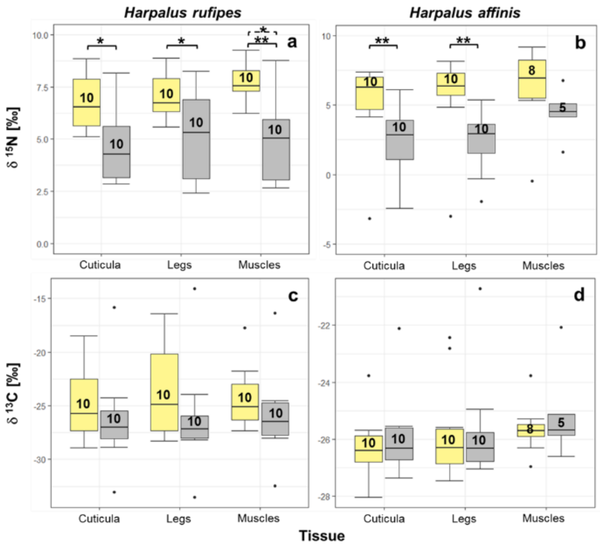


Figure 4 Stable δ ^{15}N and δ ^{13}C (in ‰) in cuticula, legs, and muscles of *Harpalus rufipes* (a; c) and *H. affinis* (b; d) from agricultural (yellow boxes) and urban (grey boxes) habitats, numbers within box plots provide sample sizes, black brackets with stars indicate significant difference between stable isotope values in tissues between habitats, dotted bracket with star indicate significant differences in variability of stable isotope values in tissues between habitats (* = $p < 0.05$; ** = $p < 0.01$).

By testing the variability of δ ^{15}N and δ ^{13}C values in different tissues of specimens, originating from agricultural or urban habitats, we found no differences for both *H. affinis* and *H. rufipes*. However, the variability of δ ^{15}N values of *H. rufipes* muscles was significantly higher in urban compared to agricultural habitats (Levene's test: muscles: $n = 20$; $df = 18$; $F = 7.969$; $p = 0.011$; Tab. A5; Fig. 4a). The comparison of nitrogen and carbon stable isotope signatures between cuticula, legs and muscles of specimens of both species either from agricultural or urban habitats yielded no significant differences (Tab. A4).

Discussion

Man-made environmental changes can affect species' traits which in reverse might enable species to persist through and beyond rapid transitions of environments. Such trait changes may occur across spatial and temporal gradients (van´t Hof et al. 2011; Doudna and Danielson 2015; Keinath et al. 2020; Niemeier et al. 2020). Our study focussed on changes in body size and isotopic signatures of two ground beetle species, *Harpalus affinis* and *H. rufipes*. Both species are common in our study region where they persisted over the past 125 years despite profound environmental change in rural and urban habitats.

Body size is often used as an indicator for habitat quality, and might provide information about habitat suitability across increasing urbanisation and agricultural intensity (Weller and Ganzhorn 2003; Sukhodolskaya 2013). In our study we hypothesized specimens of both species occurring in the city to be smaller than rural inhabitants. We further predicted body size of both species to decrease from the past to nowadays in the city, reflecting higher and increasing urban temperatures than in rural areas (Oke 1973; Tseng et al. 2018).

We found no changes in body size in both sexes of *H. affinis* and *H. rufipes'* females across space and time. However, we detected a decrease in *H. rufipes* males' body size in the city across 125 years. Males of *H. rufipes* from city areas were significantly smaller recently (2016-2017) compared to specimens from former time periods (1892-1949; 1957-1998). In many taxa intraspecific variation of body size is known to be influenced by warmer environmental temperatures, primarily in ectotherms i.e. amphibians (Reading 2007), fish (Todd et al. 2008), and insects because warmer environmental temperatures lead to shorter developmental times, resulting in smaller sizes at maturity (Atkinson 1994; Kingsolver and Huey 2008). Cities are known to exhibit higher temperatures than their rural surroundings, up to 10 degree (Oke 1973). Temperatures are also known to increase with increasing levels of urbanisation (Tseng et al. 2018). Thus, higher and/or increasing temperatures within the city were assumed to result in smaller and/or decreasing body size in both species when occurring in city, like described for other arthropods (Kotze et al. 2011; Brans et al. 2017).

However, because we only found changes in male *H. rufipes*' body size in the city across time and not in both species' females, we assume increasing urban heat to be not the main driver for these changes. Moreover, urban heat would also have an effect on both species' body size across space and would be visible in smaller sized specimens compared to specimens from rural areas. However, we did not detect any spatial intraspecific differences in body size between habitats (agricultural and urban) and areas (rural and city) in both species.

Harpalus affinis and *H. rufipes* differ in their activity pattern: *Harpalus affinis* is diurnal whereas *H. rufipes* is predominantly nocturnal (Wrase 2004). Although there is a lack of studies of intersexual differences in mating behaviour in *H. rufipes*, an evidence for male-biased dispersal was found for another ground beetle species, *Pterostichus oblongopunctatus* (Lagisz et al. 2010). Generally, among insects, males expend most of their reproductive energy as mating effort, i.e. dispersal for finding new mates, while females show less mating effort because they expend more time and energy to parental effort, i.e. egg production (Thornhill and Alcock 1983). Furthermore, *H. rufipes* is known to be attracted by artificial light sources at night (Kegel 1990; Szentkirályi et al. 2003). Thus, living in the city might be a high risk for this species due to high numbers of artificial light sources, i.e. streetlights. During dispersal *H. rufipes* males might be distracted by artificial lights at night whereas females might be less impacted. Insect body size is also dealing as an indicator for dispersal ability (Dingle et al. 1980; Derr et al. 1981). Larger sized specimens are able to disperse over longer distances due to better flight conditions and larger wings (Dingle et al. 1980; Davies 1984). Based on the increasing numbers of artificial light sources within the city of Berlin over the past 150 years as a result of increasing urbanisation (Eisenbeis and Hänel 2009; Kyba et al. 2017), larger sized males of *H. rufipes* might be deducted by artificial light sources because of their high dispersal abilities and become easy prey to predation or die due to exhaustion because they are unable to escape out of the light beam, like it was described for other nocturnal insects (Eisenbeis 2006; Manfrin et al. 2018). However, smaller males might be less affected by artificial light sources because of their less flight and dispersal abilities which might led to natural selection for smaller sized males in the city over time. Further it was shown by Crawley (1989) that larger body size within species promote success to disperse, but is offset by lower reproductive rates due to higher costs to be larger. Thus, smaller sized males of *H. rufipes* might have an adaptive advantage when occurring in the city. Additionally, it might explain why *H. rufipes* males stayed nearly constant in rural areas over the same timeframe. Rural areas are less impacted by artificial light sources

(Rich and Longcore 2006) resulting in a reduction of this selective pressure. Furthermore, it would also explain the high variation of *H. rufipes* males' body size in urban habitats and city areas in space. Even cities exhibit habitats with less or no artificial light sources (Rich and Longcore 2006).

According to that, the lack of any changes in body size of both sexes of *H. affinis* but the higher variability in males' body size in the city nowadays (2016-2017) than in the past (1892-1949) might be explained by their diurnal activity. The city of Berlin exhibits more variable habitats nowadays, providing habitats from highly urbanised to huge greenspaces, than in the past due to its development to one of the greenest cities of Europe although it became one of the highest populated cities within the same time (Schewenius et al. 2014). Thus, different predation pressure might appear on *H. affinis* males depending on their need to disperse out of an insufficient habitat what might lead to high variability in body size.

Our findings give a hint that different activity pattern of species and their sexes might play a role when adapting to altered environmental conditions. Our previous study indicates in *Harpalus affinis* a sex specific adaptation in colouration to urbanisation across the same timeframe (Keinath et al. 2020), because it might be more depending on its colouration due to its diurnal activity.

Stable isotopic signatures provide information about the living conditions of specimens, e.g. the position within the food web (Birkhofer et al. 2011) and/or the shift in the energy source of its diet (Hood-Nowotny and Knols 2007; Schallhart et al. 2009). We found higher nitrogen isotopic enrichments in both species when living in landscapes that are intensively used for agriculture than when living in urban habitats. Stable nitrogen enrichments might be higher in specimens because of their higher position within the food web (Birkhofer et al. 2011) or if its environment is highly enriched by nitrogen such as landscapes intensively used for agriculture due to the use of fertilizer (Freyer and Aly 1974; Shearer et al. 1974; DeNiro and Epstein 1980; Jenkinson 2001). Particularly, we found higher nitrogen isotopic signatures in all tissues of *H. rufipes* and in *H. affinis*' tissues that represent nutritive signatures of larval stages (Peterson and Fry 1987; Gratton and Forbes 2006) from agricultural in comparison to urban habitats.

Our findings might indicate that larvae of both species and adults of *H. rufipes* are feeding on different food sources when occurring in agricultural in comparison to urban habitats what might lead to a change in their position within food web (Birkhofer et al. 2011). However, it seems rather unlikely because of the high intensification of agriculture with application of fertilizer in our agricultural study sites. Thus, our findings rather suggest that higher environmental nitrogen enrichments have an influence on biochemistry in larval stages in both species, and in at least adult stages in *H. rufipes* due to intense application of fertilizer in our agricultural study sites. This effect was also described in a study of Birkhofer et al. (2011) and showed that nitrogen isotopic compositions in arthropods are increasing with the intensity level of agricultural land usage. However, in *H. affinis*' tissues, representing adult stage, no difference in the stable nitrogen isotope composition of specimens from agricultural and urban habitats was found and might give hint that *H. affinis* dispersed into isotopically distinct habitats after larval development. Adults of *H.*

affinis might occur in urban habitats with high nitrogen isotope ratios that might be comparable to those of intense agricultural ones.

This assumption might further be underlined by the higher variability of nitrogen isotope values in *H. rufipes* tissues, representing adult stages, in urban habitats compared to agricultural ones. Agricultural landscapes are homogenous environments because of their high amount of monocultures (Jongman 2002) whereas urban environments exhibit heterogeneous structures i.e. parks, private gardens, ruderal areas and green stripes (Gill and Bonnett 1973; Lussenhop 1973; Tischler 1973; Falk 1976). These heterogeneous structures are also variable in nitrogen enrichment (Pyšek 1995), depending on the degree of anthropogenic impact: Nearby streets, caused by automobile exhaust (Baker et al. 2001), the use of chemical fertilizer for maintaining lawns (Muchovej and Rechcigl 1994), the ecosystem structure of the city and the deposit of excretions of pets in lawns and byways (Zhu et al. 2004).

Increased nitrogen isotopic variability was also found in the European Common Frog when occurring in non-agricultural in comparison to agricultural landscapes within the Berlin-Brandenburg region (Niemeier et al. 2020). Thus, highly human induced habitats within the city might be also reflected in higher stable nitrogen isotopic enrichments within specimens' tissues.

Contrary to the effects we found for nitrogen isotopes, we found no significant differences in carbon signatures in both species' tissues between agricultural and urban habitats. Thus, we are not able to make any additional assertion about dispersal of *H. affinis* between isotopically distinct habitats.

However, in *H. rufipes* higher carbon isotope signatures were visible when occurred in agricultural in comparison to urban habitats. Although this effect was not significant, it might be explained by the higher proportion of C4 than C3 plants, like corn, in arable fields than in the city (Degens 1969; Schwarcz 1969). However, because carbon isotope signatures provide information about the respective energy base of species food sources (DeNiro and Epstein 1978; Ponsard and Arditi 2000; Gratton and Forbes 2006), the absence of any significant differences might indicate that the energy base stayed the same in both habitats.

Although agricultural environments are highly enriched by nitrogen, some urban habitats are assumed to have similar high nitrogen values like described by Pyšek (1995), what is reflected in species' tissues. However, stable carbon isotope enrichments in our study species showed that their energy base did not differ between agricultural and urban habitats and beetles' life stages (Gratton and Forbes 2006).

References

Anjum-Zubair M, Entling MH, Bruckner A, Drapela T, Thomas F (2015) Differences of spring carabid beetle assemblages between semi-natural and adjoining winter wheat. Agricultural and Forest Entomology 17:355-365.https://doi.org/10.1111/afe.12115

Antrop M (2000) Changing patterns in the urbanized countryside of Western Europe. Landscape Ecology 15:257-270. https://doi.org/10.1023/A:1008151109 252

Antrop M (2004) Why landscapes of the past are important for the future. Landscape and Urban Planning 70:21-34. https://doi.org/10.1016/j.landu rb plan.2003.10.002

Atkinson D (1994) Temperature and organism size – A biological law for ectotherms? Advances in Ecological Research 25:1-58.

Bairoch P, Goertz G (1986) Factors of urbanisation in the nineteenth century developed countries: A descriptive and econometric analysis. Urban Studies 23:285-305 https://doi.org/10.1080/00420988620080351

Baker LA, Hope D, Xu Y, Edmonds J, Lauver L (2001) Nitrogen balance for the central Arizona–Phoenix (CAP) ecosystem. Ecosystems 4:582-602. https://doi.org/10.1007/s10021-001-0031-2

Bažok R, Kos T, Igrc Barčić J, Kolal V, Lazarević B, Čatić A (2007) Abundance and distribution of the ground beetle *Pterostichus melanarius* (Illiger, 1798) and *Pseudoophonus rufipes* (De Geer, 1774) in corn fields in Croatia. Entomologia Croatica 11:39-51. https://hrcak.srce.hr/39510

Birkhofer K, Fließbach A, Wise HD, Scheu S (2011) Arthropod food webs in organic and conventional wheat farming systems of an agricultural long term experiment: A stable isotope approach. Agricultural and Forest Entomology 13:197-204. https://doi.org/10.1111/j.1461-9563.2010.00511.x

Brans KI, Jansen M, Vanoverbeke J, Tüzün N, Stoks R, De Meester L (2017) The heat is on: Genetic adaptation to urbanization mediated by thermal tolerance and body size. Global Change Biology 23:5218-5227. https://doi.org/10.1111/gcb.13784

Buesch O, Haus W (1987) Berlin als Hauptstadt der Weimarer Republik 1919-1933. Walter de Gruyter and Co, Berlin.

Crawley MJ (1989) Chance and timing in biological invasions. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejma´nek, M, Williamson M (eds) Biological invasions, a global perspective. John Wiley and Sons, Chichester, pp 407-423

Cochrane A, Jonas A (1999) Reimagining Berlin: World city, national capital or ordinary place? European Urban and Regional Studies 6:145-164. https://doi.org/10.1177/096977649900600204

Cook LM, Saccheri IJ (2013) The peppered moth and industrial melanism: Evolution of a natural selection case study. Heredity 110:207-212. https://doi.org/10.1038/hdy.2012.92

Davies AM (1984) The flight and migration ecology of the Red Milkweed Beetle (*Tetraopes tetraophthalmus*). Ecology 65:230-234. https://doi.org/10.2307/1939475

Degens ET (1969) Biogeochemistry of stable carbon isotopes. In: Eglinton G, Murphy MTJ (eds) Organic Geochemistry, 1st edn. Springer, Berlin, pp 304-329

Deichsel, R (2006) Species change in an urban setting - ground and rove beetles (Coleoptera: Carabidae and Staphylinidae) in Berlin. Urban Ecosystems 9:161-178. https://doi.org/10.1007/s11252006-8588-3

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:495-506. https://doi.org/10.1016/0016-7037(78)90199-0

DeNiro MJ, Epstein S (1980) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica Cosmochimica Acta 45:341-351. https://doi.org/10.1016/0016-7037(81)90244-1

Derr JA, Alden B, Dingle H (1981) Insect life histories in relation to migration, body size, and host plant array: A comparative study of Dysdercus. Journal of Animal Ecology 50:181-194. https://doi.org/10.2307/4039

Dingle H, Blakeley NR, Miller ER (1980) Variation in body size and flight performance in milkweed bugs (Oncopeltus). Evolution 34:372-385. https://doi.org/10.2307/2407400

Dinno A (2017) R Package 'dunn.test'. Dunn's Test of Multiple Comparisons Using Rank Sums.

Doudna JW, Danielson BJ (2015) Rapid morphological change in the masticatory structures of an important ecosystem service provider. PLOS ONE 10(6) e0127218. https://doi.org/10.1371/journal.pone.0127218

Eisenbeis G (2006) Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. In: Rich C, Longcore T (eds) Ecological Consequences of Artificial Night Lighting. Island Press, Washington D. C., pp 281-304

Eisenbeis G, Hänel A (2009) Light pollution and the impact of artificial night lighting on insects. In: McDonnell MJ, Hahs AH, Breuste HJ (eds) Ecology of Cities and Towns. Cambridge University Press, Cambridge, pp 243-263

Erisman JW, Sutton MA, Galloway J, Klimont Z, Winiwarter W (2008) How a century of ammonia synthesis changed the world. Nature Geoscience 1:636-639. https://doi.org/10.1038/ngeo325

Falk JH (1976) Energetics of a suburban lawn ecosystem. Ecology 57:141-150.https://doi.org/10.2307/1936405

Freyer HD, Aly A (1974). Nitrogen-15 variations in fertilizer nitrogen. Journal of Environmental Quality 3:405-406. https://doi.org/10.2134/jeq1974.00472425000300040023x

Gill D, Bonnett P (1973) Nature in the Urban Landscape. A Study of City Ecosystems. York Press, York

Giraudeau, M., Nolan, P. M., Black, C. E., Earl, S. R., Hasegawa, M., & McGraw, K. J. (2014). Song characteristics track bill morphology along a gradient of urbanization in house finches (*Haemorhous mexicanus*). Frontiers in Zoology 11 Article number 83. https://doi.org/10.1186/s12983-014-0083-8

Gratton C, Forbes E (2006). Changes in δ13C stable isotopes in multiple tissues of insect predators fed isotopically distinct prey. Oecologia 147:615-624. https://doi.org/10.1007/s00442-005-0322-y

Harris JA, Hobbs RJ, Higgs E, Aronson J (2006) Ecological restoration and global climate change. Restoration Ecology 18:170-176. https://doi.org/10.1111/j.1526-100X.2006.00136.x

Harrison S, Gallandt ER (2012) Behavioural Studies of *Harpalus rufipes* De Geer: an important weed seed predator in Northeastern US agroekosystems. International Journal of Ecology 846546. https://doi.org/10.1155/2012/846546

Hobbs RJ, Higgs ES, Hall C (2013) Novel ecosystems: Intervening in the new ecological world order. Wiley-Blackwell, New Jersey. https://doi.org/10.1002/9781118354186

Holec V, Mišurcová J, Tuf IH, Veselý M (2006) Soil invertebrates (Coleoptera: Carabidae; Isopoda: Oniscidea) of the floodplain forest mosaic. Environmental changes and biological assessment III. Scripta facultatis rerum naturalium Universitatis Ostravensis 163:242-248.

Hood-Nowotny R, Knols BGJ (2007) Stable isotope methods in biological and ecological studies of arthropods. Entomologia Experimentalis et Applicata 124:3-16. https://doi.org/10.1111/j.1570-7458.2007.00572.x

Jeltsch F, Blaum N, Brose U et al. (2013) How can we bring together empiricists and modellers in functional biodiversity research? Basic and Applied Ecology 14:93-101. https://doi.org/10.1016/j.baae.2013.01.001

Jenkinson SD (2001) The impact of humans on the nitrogen cycle, with focus on temperate arable agriculture. Plant and Soil 228:3-15. https://doi.org/10.1023/A:1004870606003

Jongman RHG (2002) Homogenisation and fragmentation of the European landscape: Ecological consequences and solutions. Landscape and Urban Planning 58:211-221. https://doi.org/10.1016/S016 92046(01)00222-5

Kavanaugh DH (1979). Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic Nebrza species and subspecies. Proceedings of the California Academy of Science 42:87-133.

Kegel B (1990) Diurnal activity of carabid beetles living on arable land. In: Stork NE (ed) The Role of Ground Beetles in Ecological and Environmental Studies. Andover Intercept, London, pp 65-76

Keinath S, Frisch J, Müller J, Mayer F, Rödel M-O (2020) Spatio-temporal color differences between urban and rural populations of a ground beetle during the last 100 years. Frontiers in Ecology and Evolution – Urban Ecology 7:525. https://doi.org/10.3389/fevo.2019.00525

Kenis M, Auger-Rozenberg MA, Roques A, Timms L, Péré C, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. Biological Invasions 11:21-45. https://doi.org/10.1007/s10530-008-9318-y

Kingsolver J, Huey RB (2008) Size, temperature, and fitness: three rules. Evolutionary Ecology Research 10:251-268.

Kotze DJ, O'Hara RB (2003) Species decline - but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. Oecologia 135:138-148. https://doi.org/10.1007/s00442-002-1174-3

Kotze J, Venn S, Niemelae J, Spence J (2011) Effects of urbanization on the ecology and evolution of arthropods. In: Niemelae J, Breuste JH, Elmqvist T, Guntenspergen G, James P, McIntyre EN (eds) Urban Ecology: Patterns, Processes, and Applications. Oxford Univ Press, Oxford, pp 159-166

Kratke S (2000) Berlin: the metropolis as a production space. European Planning Studies 8:7-27. https://doi.org/10.1080/096543100110901.

Kyba CMC, Kuester T, Kuechly UH (2017) Changes in outdoor lighting in Germany from 2012-2016. International Journal of Sustainable Lighting 19:112-123. https://doi.org/10.26607/ijsl.v19i2.79

Lagisz M, Wolff K, Sanderson AR, Laskowski R (2010) Genetic population structure of the ground beetle, *Pterostichus oblongopunctatus*, inhabiting a fragmented and polluted landscape: Evidence for sex-biased dispersal. Journal of Insect Science 10:105. https://doi.org/10.1673/031.010.10501

Lindroth CH (1949) Die Fennoskandischen Carabidae. III. Allgemeiner Teil. Göteborgs kungliga Vetenskaps- och Vitterhets- Samhälles Handlingar Serie B 4:1-911

Lussenhop J (1973) The soil arthropod community of a Chicago expressway margin. Ecology 54:1124-1137. https://doi.org/10.2307/1935579

Manfrin A, Lehmann D, van Grunsven HAR, Larsen S, Syväranta J, Wharton G, Voigt CC, Monaghan TM, Hölker F (2018) Dietary changes in predators and scavengers in a nocturnally illuminated riparian ecosystem. Oikos 127:960-969. https://doi.org/10.1111/oik.04696

Mariotti A (1983) Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. Nature 303:685-687.

Muchovej MCR, Rechcigl EJ (1994) Impact of nitrogen fertilization pastures and turfgrasses on water quality. In: Steward AB (ed.) Soil processes and water quality, 1st edn. CRC Press, Florida, pp 91-136

Niemeier S, Müller J, Struck U, Rödel M-O (2020) Superfrogs in the city: 150 year impact of urbanization and agriculture on the European Common Frog. Global Change Biology 26:6729-6741. https//doi.org/10.1111/gcb.15337

Niemelae J, Kotze DJ, Venn S, Penev L, Stoyanov I, Spence J, Hartley D, de Oca AM (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. Landscape Ecology 17:387-401. https://doi.org/10.1023/A:1021270121630

Ogle D, Wheeler P, Dinno A (2019) R Package FSA. Simple Fisheries Stock Assessment Methods. https://github.com/droglenc/FSA

Oke TR (1973) City size and the urban heat island. Atmospheric Environment 7:769-779. https://doi.org/10.1016/0004-6981(73)90140-6

Palkovacs EP, Kinnison TM, Correa C, Dalton MC, Hendry PA (2011) Fates beyond traits: Ecological consequences of human-induced trait change. Evolutionary Applications 5:183-191.https://doi.org/10.1111/j.1752-4571.2011.00212.x

Pamme H (2003) Das Politikfeld Umweltpolitik. In: Grunow D (ed) Verwaltungshandeln in Politikfeldern, 1st edn. Leske and Budrich, Opladen, pp 185-224

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology, Evolution, and Systematics 18:293-320.https://doi.org/10.1146/annurev.es.18.110187.001453

Ponsard S, Arditi R (2000) What can stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) tell about the food web of soil macro-invertebrates? Ecology 81:852-864. https://doi.org/10.1890/0012-9658(2000)081[0852:WCSINA]2.0.CO; 2

Pyšek P (1995) Approaches to studying spontaneous settlement flora and vegetation in central Europe. In: Sukopp H, Numata M, Huber A (eds) Urban Ecology as the Basis of Urban Planning. SPB Academic Publishing, Warsaw, pp 23-39

R Core Team (2017) R: A language and environment statistical computing. R Foundation for Statistical Computing, Vienna, URL http://www.R-project.org/

Reading CJ (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. Oecologia 151:125-131. https://doi.org/10.1007/s00442-006-0558-1

Reif H (2003) Dynamics of Sub-urbanisation - The Growing Periphery of the Metropolis. Berlin 1890 - 2000. In: van Dijk H (ed) The European Metropolis 1920-2000. http://hdl.handle.net/1765/1020

Ribbe W, Bohm E, Schich W, Schulz K (2002a) Geschichte Berlins. Band 1: Von der Frühgeschichte bis zur Industrialisierung. Beck, Munich

Ribbe W, Bohm E, Schich W, Schulz K (2002b) Geschichte Berlins. Band 2: Von der Märzrevolution bis zur Gegenwart. Beck, Munich

Ricciardi A (2007) Are modern biological invasions an unprecedented form of global change? Conservation Biology 21:329-336. https://doi.org/10.1111/j.1523-1739.2006.00615.x

Rich C, Longcore T (2006) Ecological Consequences of Artificial Night Lighting. Island Press, Washington

Rocha LA, Aleixo A, Allen G, Almeda F, Baldwin CC, Barclay LVM et al. (2014) Specimen collection: an essential tool. Science 344:814-815.https://doi.org/10.1126/science.344.6186.814

Root TL, Schneider HS (2006) Conservation and climate change: The challenges ahead. Conservation Biology 20:706-708. https://doi.org/10.1111/j.1523-1739.2006.00465.x

Rosing MN, Ben-David M, Barry PR (1998) Analysis of stable isotope data: A K Nearest-Neighbors Randomization Test. Journal of Wildlife Management 62:380-388. https://doi.org/10.2307/3802302

Schallhart N, Wallinger C, Juen A, Traugott M (2009) Dispersal abilities of adult click beetles in arable land revealed by analysis of carbon stable isotopes. Agricultural and Forest Entomology 11:333-339. https://doi.org/10.1111/j.1461-9563.2009.00428.x

Schewenius M, McPhearson T, Elmqvist T (2014) Opportunities for increasing resilience and sustainability of urban social-ecological systems: Insights from the URBES and the Cities and Biodiversity Outlook Projects. Ambio 43:434-444. https://doi.org/10.1007/s1328 0-014-0505-z

Schildt A, Sywotlek A (1993) Modernisierung im Wiederaufbau. In: Dietz WHJ (ed) Die westdeutsche Gesellschaft der 50er Jahre. Nachf GmbH, Bonn

Schwarcz HP (1969) The stable isotopes of carbon. In: Wedepohl KW (ed) Handbook of Geochemistry. Springer, Berlin, pp 1-16

Shearer GB, Kohl DH, Commoner B (1974) The precision of determinations of the natural abundance of nitrogen-15 in soils. Fertilizers, and shelf chemicals. Soil Science 118:308-316.

Sota T, Takami Y, Kubota K, Ujiie M, Ishikawa R (2000) Interspecific body size differentiation in species assemblages of the carabid subgenus Ohomopterusin Japan. Population Ecology 42:279-291. https://doi.org/10.1007/PL00012006

Sukhodolskaya RA (2013) Intraspecific body sizes variation in ground beetles (Coleoptera, Carabidae) in urban–suburban–natural gradient. Acta Biologica Universitatis Daugavpiliesis 13:121-128. ISSN 1407-8953

Sunderland KD, Loevei GL, Fenlon J (1995) Diets and reproductive phenologies of the introduced ground beetles *Harpalus affinis* and *Cilvina australasiae* (Coleoptera: Carabidae) in New Zealand. Australian Journal of Zoology 43:39-50. https://doi.org/10.1071/ZO9950039

Sustek Z (1992) Changes in representation of carabid life forms along an urbanization gradient (Coleoptera, Carabidae). Biologia (Bratislava) 47:417-430

Szentkirályi F, Bernáth B, Kádár F, Retezár I (2003) Flight of ground beetles towards polarized and unpolarised light sources. European Carabidology 114:313-324.

Thiele HU (1977) Carabid beetles in their environments. Springer, Berlin

Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge

Tilman D, Cassman GK, Matson PA, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. Nature 418:671-677. https://doi.org/10.1038/nature01014

Tischler W (1973) Ecology of arthropod fauna in man-made habitats: The problem of synanthropy. Zoologischer Anzeiger 191:157-161.

Todd CD, Hughes SL, Marshall CT, MacLean JC, Lonergan ME, Biuw EM (2008) Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. Global Change Biology 14:958-970. https://doi.org/10.1111/j.1365-2486.2007.01522.x

Toft S, Bilde T (2002) Carabid diets and food value. In: Holland MJ (ed) The agroecology of carabid beetles. Intercept limited, Andover, pp 81-110.

Townsend JI (1992) *Harpalus affinis* (Schrank) (Coleoptera: Carabidae) recently established in the North Island of New Zealand. New Zealand Entomologist 15:25-29. https://doi.org/10.1080/00779962.1992.972264

Trautner J (2017) Die Laufkäfer Baden-Württembergs, Band 2: Spezieller Teil II. Ulmer, Stuttgart

Tseng M, Kaur KM, Pari SS, Sarai K, Chan D, Yao CH, Porto P, Toor A, Toor HS (2018) Decrease in beetles body size linked to climate change and warming temperatures. Journal of Animal Ecology 87:647-659. https://doi.org/10.1111/1365-2656.12789

UBA (1998) Umweltdaten Deutschland 1998. Umweltbundesamt. Erich Schmidt, Berlin

UNEP/WHO (1993) City air quality trends. Vol. 2. WHO PEP/93 26, UNE93 26P GEMS 93.A.2. Geneva, 1993

United Nations (2018) Department of Economic and Social Affairs, Population Division. The World's Cities in 2018-Data Booklet.

Van't Hof A, Edmonds E, Dalikova M, Marec F, Saccheri JI (2011) Industrial melanism in British Peppered Moths has a singular and recent mutational origin. Science 332:958-960. https://doi.org/10.1126/science.1203043

Weller B, Ganzhorn UJ (2003) Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. Basic and Applied Ecology 5:193-201. https://doi.org/10.1078/14391791-00220

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer, Berlin

Wrase DW (2004) Harpalina in Die Käfer Mitteleuropas: In: Freude H, Harde WK, Lohse AG, Klausberger B, Müller-Motzfeld G (eds) Adephaga 1 Carabidae (Laufkäfer). Spektrum, Heidelberg

Zhu W-X, Dillard DN, Grimm BN (2004) Urban nitrogen biogeochemistry: status and process in green retention basins. Biogeochemistry 71:177-196. https://doi.org/10.1007/s10533-004-9683-2

Ziegler J (2011) Recent range extensions of tachinid flies (Diptera: Tachinidae, Phasiinae) in north east Germany and a review of the overall distribution of five species. Studia Dipterologica 18:29-54. ISSN 0945-3954.

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5.3 Paper 3

Spatio-temporal color differences between urban and rural populations of a ground beetle during the last 100 years

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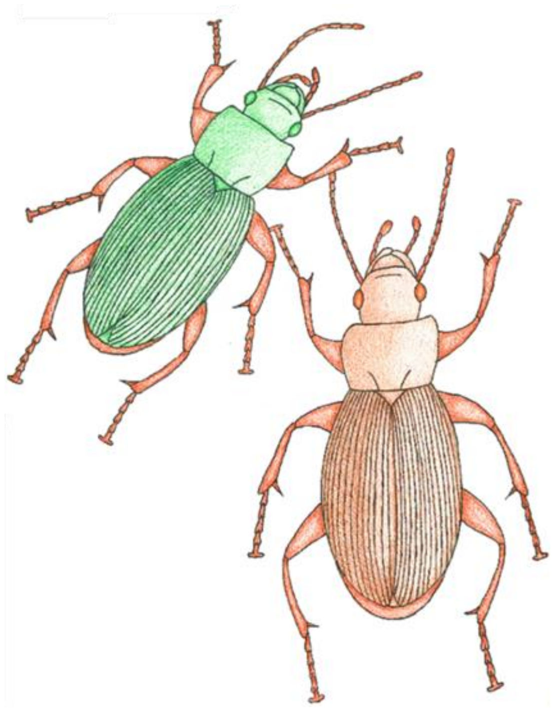

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Spatio-Temporal Color Differences Between Urban and Rural Populations of a Ground Beetle During the Last 100 Years

Silvia Keinath[1,2], Johannes Frisch[1], Johannes Müller[1,2], Frieder Mayer[1,2] and Mark-Oliver Rödel[1,2]*

[1] Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany, [2] Berlin-Brandenburg Institute of Advanced Biodiversity Research – BBIB, Berlin, Germany

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***Correspondence:**
Silvia Keinath
silvia.keinath@mfn.berlin

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Increasing anthropogenic environmental impacts lead to rapid transitions of ecosystems and species. Species persisting in changing environments may respond to changes by altering phenotypic traits across space and/or time. Here we tested whether the frequencies of three color morphs in the ground beetle *Harpalus affinis* differed across spatial and temporal gradients. The gradients extended from urban to rural regions, and from the early twentieth century until today, in the Berlin-Brandenburg area, Germany. Specimens comprised beetles from the entomological collection of the Museum für Naturkunde, Berlin and recently collected material. As a result of differing environments, we expected to observe differences in color frequencies in beetles between habitats and across time, responding to different levels of urbanization. Our results revealed sexual dichromatism in *H. affinis* as well as some habitat dependent differences in trait frequency. Frequencies of color morphs remained generally constant in males across space and time. Females likewise showed no differences in color frequencies between habitats, urban and rural regions, and between different time periods in rural regions. In contrast color morph frequencies changed in urban regions over time in females: Bronze color decreased, whereas green color became more dominant over time. We assume that bronze color was selectively advantageous in times with high levels of soot pollution in the city, whereas green is more cryptic and thus advantageous in times with less polluted air. The color change of females thus could have been driven by natural selection. In contrast, the persistence of predominately green males through all times and habitats, more likely can be explained by sexual selection.

Keywords: color, urbanization, novel ecosystems, museum collection, ground beetle, *Harpalus affinis*

INTRODUCTION

Increasing levels of urbanization and agricultural land use, mostly due to rapid population growth (Bairoch and Goertz, 1986; Antrop, 2004), cause rapid environmental transitions from natural to degraded or novel ecosystems and thus are of major ecological and socio-economic interest (Hobbs et al., 2013; Jeltsch et al., 2013). Novel ecosystems are defined as systems that differ in their (species) composition and/or function from present and past systems due to anthropogenic impacts such as land use and climate change (Harris et al., 2006; Root and Schneider, 2006; Ricciardi, 2007). Due to human induced environmental changes (**Figure 1**), the native fauna and flora will be heavily impacted by habitat degradation, fragmentation, and conversion, as well as the invasion of new species, and the creation of new habitats (Ribera et al., 2001; Haila, 2002). Consequently, many native species will be lost (Maas et al., 2002; Brunk and Wiegleb, 2006; Kenis et al., 2009; Ziegler, 2011). However, there are some native species that persist throughout these environmental transitions (Van't Hof et al., 2011; Doudna and Danielson, 2015). How these species deal with the changing environments, especially if rapid transitions triggered any changes in their phenotypes or if particular (pre-)adaptations enable these species to persist, whilst other species disappeared (Palkovacs et al., 2011), has been so far mostly neglected.

Whereas changes in behavior and physiology usually cannot be directly assessed over long time periods, certain morphological traits may be collected from time series of preserved specimens in historical collections (Rocha et al., 2014; Doudna and Danielson, 2015). Morphological traits that are known to be influenced by environmental conditions are body size (Sustek, 1992; McCabe and Patridge, 1997; Ribera et al., 2001), body proportions (Atkinson, 1994), including fluctuating asymmetry (Palmer and Strobeck, 1992), and coloration (Schultz and Rankin, 1985). These traits can be used as proxies for a species' ecological and physiological modification during its adaptation to a novel ecosystems. The historical datasets can finally be completed with recent samples to cover spatio-temporal gradients across environmental transitions (Van't Hof et al., 2011; Doudna and Danielson, 2015).

Coloration is often related to background matching (Cott, 1940; Kettlewell, 1956; Endler, 1984, 1988; Storfer et al., 1999), and represents a trait that may change due to urbanization (Harrison and Garrett, 1926; Kettlewell, 1955, 1956; Clarke and Sheppard, 1966; Bishop, 1972). Most colors, based on pigments, fade after death (Doucet and Hill, 2009). By contrast structural colors like multilayer reflectors, as often found in Coleoptera (Parker, 1998; Noyes et al., 2007; Kinoshita et al., 2008), develop during metamorphosis by secretion of thin parallel layers of chitin by the epidermis and harden during sclerotization. One or more colors will be produced by constructive interference if the spacing of these layers approaches the wavelength of visible light (Land, 1972). Because these colors are depending on structure and not on pigments, they retain their properties under normal museum conditions (Parker and McKenzie, 2003). This makes

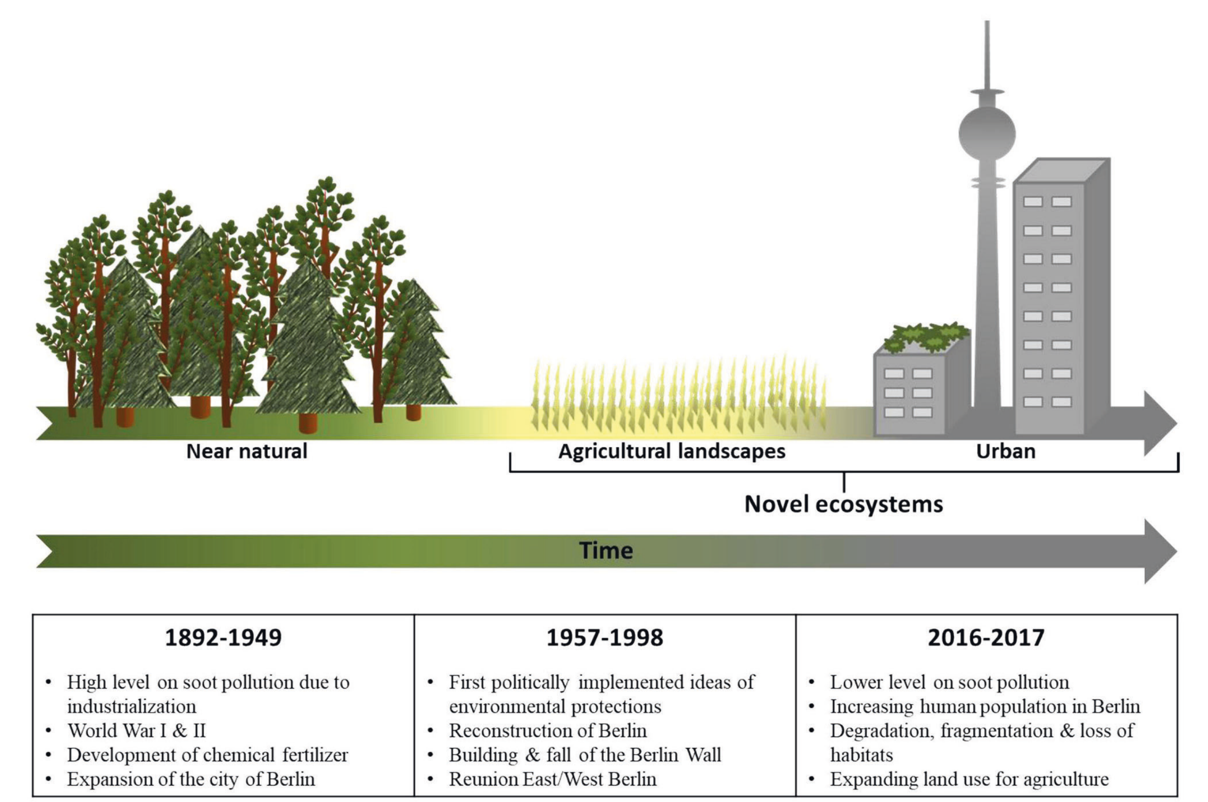

FIGURE 1 | History and anthropogenic impacts on environments in space and time in the German Berlin-Brandenburg area. Different habitat types nowadays in space are reflected over time. Important events influencing environments are connected with the respective time period.

them a useful trait for spatial and temporal comparisons (Hadley et al., 1988; Tyler, 2010).

One species that is characterized by multilayer reflectors and occurs in three distinctly different metallic color morphs (Seago et al., 2009) is the ground beetle *Harpalus affinis*. It is a well-known insect species persisting in natural and modified habitats such as agricultural fields (Sunderland et al., 1995), semi-natural landscapes (Anjum-Zubair et al., 2015), natural landscapes (Townsend, 1992), and urban green spaces (Deichsel, 2006).

The aim of this study was to investigate whether or not *H. affinis* exhibit changes in frequencies of color morphs across space (rural to urban and between different habitat types) and time (past to now) in the Berlin-Brandenburg area of Germany. This area is characterized by increasing levels of urbanization in which rapid transitions, from near natural to novel ecosystems occur(ed) (Cochrane and Jonas, 1999). The city of Berlin is a fast-growing metropolis, whose expansion and population increase started toward the end of the nineteenth century, including a phase of rapid reconstruction in the direct aftermath of World War II (Kraetke, 2000). This led to a high level of urbanized habitats (Antrop, 2000). Berlin is surrounded by the German federal state of Brandenburg, which, in contrast to Berlin, mostly consists of rural landscapes with habitats ranging from near natural to intensively managed agricultural monocultures (Cochrane and Jonas, 1999). For our study species, we predicted differences in color frequencies between urban, agricultural and near natural habitats as well as between urban and rural regions. We further predicted changes in color frequencies in rural and urban regions over time, spanning the end of the nineteenth century until nowadays. Color differences and changes should emerge depending on the respective level of land use and urbanization in the respective habitat, region and time, responding in higher frequencies of dark morphs in habitats and times with higher levels of urbanization and higher frequencies of green morphs in less urbanized habitats, regions and times.

MATERIALS AND METHODS

Study Species

The ground beetle *Harpalus affinis* (Schrank, 1781) (Coleoptera, Carabidae) is a Palearctic species (Wrase, 2004). The medium-sized (8.5–12 mm), diurnal, predominantly phytophagous species, is occasionally also preying on insect larvae (Townsend, 1992; Sunderland et al., 1995). Adults are winged and volant (Townsend, 1992), and may occur in either of three metallic color morphs: uniform metallic green, uniform bronze, or a mixture of green and bronze body parts (Wrase, 2004; **Figure 2**). Males differ from females by wider tarsal segments of the pro- and mesothoracic legs (Townsend, 1992; Loevei and McCambridge, 2002). Because this species persisted in our study area over time, occurs in different habitat types and different color morphs, and lastly is well presented in the collection of the Museum für Naturkunde, Berlin, it is a particularly well suited study species for our research question.

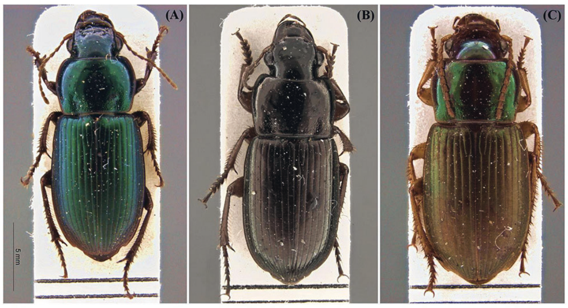

FIGURE 2 | Photographs of the three *Harpalus affinis* color morphs "green," "bronze," and "mixed," from the collections of the Museum für Naturkunde, Berlin. **(A)** (green ♀): Berlin, Prenzlauer Berg, Oderbruchkippe, 17, June 1972. **(B)** (bronze ♂): Brandenburg, nature reserve Mallnow near Seelow, 24, August 1975. **(C)** (mixed ♀): Berlin, Prenzlauer Berg, Oderbruchberg, 24, August 1969.

Origin of Specimens

Museum Vouchers

In total 546 vouchers, deposited in the Coleoptera collection of the Museum für Naturkunde, Berlin have been examined for this study. They originate from the Berlin-Brandenburg area, Germany, and span the years 1892–1998. Urban (Berlin) beetles with habitat information available have been collected at ruderal sites, dumpsites, roadsides, garden plots, and parks. Vouchers from rural Brandenburg with habitat information stem from meadows and forest edges (Appendix A in **Supplementary Material**). For some vouchers only rough information about their origin (Berlin or Brandenburg) were available. These beetles were only used for comparisons between regions and for temporal comparisons within regions and were excluded from comparisons between specific habitat types.

Recently-Collected Specimens

In total 114 recently collected specimens were used for this study. Specimens, collected in rural districts of Brandenburg were originated from agricultural winter wheat and soy fields and from fallow, grass strips in between these fields, located in: Nordwestuckermark (May to June 2016), Uckermark (June 2017), Maerkisch-Oderland (May to July 2017), and on dry grasslands in Blankenfelde-Mahlow of Teltow-Flaeming (June to July 2017). Specimens from urban sites were collected within the city of Berlin on 18 dry grassland sites (June to July 2017; Appendix A in **Supplementary Material**). These sites were comparable to sites from urban museum vouchers because dry grassland sites were located in the midst of the city. In general, due to classification into similar regions and habitats, we made sure that habitat types of specimens nowadays were comparable with those of vouchers from the collection. Specimens were collected with pitfall traps by ourselves and by cooperation partners.

Coloration Assessment

The colors of thorax and abdomen were assessed for females and males separately. If the colors of both body parts were identical, we classified the respective individual as "green" or "bronze." When thorax and abdomen were differently colored, we classified the specimen as "mixed." Color categorization were always assessed under the same light conditions and by the same person, categories were unambiguous (**Figure 2**), and were made blind as to the origin of the specimen.

Data Classification

A total of 660 of *H. affinis* from the Berlin-Brandenburg area were examined for this study: 546 from the collection of the Museum für Naturkunde, Berlin, covering a 106 year time period (1892–1998), 77 specimens collected in 2016 and 2017 from agricultural winter wheat fields, soy fields and small green spaces in between these fields in Brandenburg, and 37 beetles originated from urban habitats in Berlin (**Table 1**).

Each *H. affinis* specimen was classified according to sex, color, and origin. Specimens originated from the city of Berlin were classified as "urban." Beetles originated from its campestral surrounding, Brandenburg, were classified as "rural." These classifications were used for observations between regions and within regions over time. If habitat information of the museum vouchers were available, specimens were used for observations between different habitat types. Specimens from the rural region, Brandenburg, were further classified as originated from "agricultural landscapes" or, when sampled in protected landscapes or nature conservation areas, as originated from "near natural" habitats. Specimens from the urban region, Berlin, were used for observations between habitats when further habitat information were given that individuals were sampled in ruderal sites, dumpsites, roadsides, garden plots or parks (Appendix A in **Supplementary Material**).

For observations over time urban and rural, beetles were divided into three time periods from 1892 to 1949, 1957 to 1998, or 2016 to 2017. No sampling material was existing for times from 1999 to 2015, therefore this time period could not be included. Time period classification was based on a combination of practical reasons (availability of sufficient numbers of beetles) and biological relevance. During the first time period, the Berlin-Brandenburg area was mainly impacted by the effects of industrial revolution and the First and Second World War. Numerous newly established factories resulted in intense air pollution in Berlin (Wey, 1982; Ribbe et al., 2002a,b). Due to the development of the Haber-Bosch process for fixing nitrogen in the 1920's (Erisman et al., 2008), chemical fertilizers were for the first time applied in large quantities. These developments led to a high level of environmental pollution at that time without attempts of environmental protection (Pamme, 2003). Furthermore, Berlin was expanded to "Groß-Berlin" in the 1920's, population size exceeding the current state and leading to rapid construction of buildings and infrastructures (Buesch and Haus, 1987). During the period from 1957 to 1998, Berlin's reconstruction after World War II was finalized (Schildt and Sywottek, 1993). At the end of the 1950's, first measures concerning environmental protection were implemented (Pamme, 2003), resulting in decreasing emissions of air pollutants (UNEP/WHO, 1993; UBA, 1998), and reduced application of chemical fertilizers in the surroundings of the city (Tilman et al., 2002; Erisman et al., 2008). Therefore, this time period can be considered

TABLE 1 | Total number of *Harpalus affinis* investigated for this study.

		Total	**660**					
		Sex	**Females**			**Males**		
		Total per sex	**267**			**393**		
		Color morphs	**Green**	**Bronze**	**Mixed**	**Green**	**Bronze**	**Mixed**
		All	**137**	**59**	**71**	**237**	**129**	**27**
Spatial	Region	Berlin (urban)	61	27	28	102	60	15
		Brandenburg (rural)	76	32	43	135	69	12
	Habitat	Urban	18	5	6	27	12	4
		Agriculture	21	7	6	18	14	3
		Near natural	9	4	6	25	9	2
Temporal	Urban over time	Berlin 1892–1949	11	13	5	24	15	2
		1957–1998	42	13	20	64	37	10
		2016–2017	8	1	3	14	8	3
	Rural over time	Brandenburg 1892–1949	17	7	15	26	20	2
		1957–1998	37	18	18	88	35	7
		2016–2017	22	7	10	21	14	3

For analyses, specimens were allocated according to sex, coloration (green, bronze, mixed), regions (Berlin, Brandenburg), habitats (urban, agricultural, and near natural), and time (three periods in between the time from 1892 to 2017).

as an intermediate stage of environmental pollution due to urbanization between time period one and today. From 1999 to today, the human population within Berlin has been again steadily increasing (United Nations, 2002), but air pollution, mostly due to soot, decreased since industrialization because of environmental protection measures (UNEP/WHO, 1993; UBA, 1998; SenStadtWohn, 2018).

Statistical Analyses

For statistical analyses, every beetle was tagged by region (urban, rural), habitat type (urban, agricultural, near natural), time period (1892–1949, 1957–1998, 2016–2017), and color (green, bronze, mixed). We used the R- Project, version 3.4.0 (R Core Team, 2017) with the package RVAideMemoire (Hervé, 2013). For the analysis of the differences between color composition between habitats, regions and regions over time, the G-test of independence was used (see Forsman and Shine, 1995; Cahan et al., 2002). To examine if there were differences in color frequencies between different habitats, regions and time periods of a region, and to investigate if there were frequency differences of colors within the same habitat, region and time period per region, the pairwise G-test with Bonferroni correction for multiple testing was used.

RESULTS

Across all vouchers, we observed significant differences in the frequencies of color morphs between sexes (G = 15.505, df = 2, $p < 0.001$). Females showed significantly more often "mixed" colors than males ($p < 0.001$). The frequencies of "green" and "bronze" colors did not differ between sexes. Significantly more females were "green" compared to "bronze" ($p = 0.002$) or "mixed" ($p = 0.019$). Males likewise were more often "green" than "bronze" ($p = 0.014$) or "mixed" ($p < 0.001$). "Bronze" males occurred more often than "mixed" ($p < 0.001$) ones (**Figure 3**). Both sexes also partly exhibited different frequencies of color morphs with regard to habitat type, region and region over time.

In females we observed no differences in coloration between urban, agricultural and near natural habitats (G = 4.8017; df = 4, $p = 0.308$). However, in urban habitats "green" dominated over "bronze" ($p < 0.001$) and "mixed" ($p < 0.001$) ones. In agricultural habitats frequencies of "green" were higher than "bronze" ($p < 0.001$) and "mixed" ones ($p = 0.002$). In near natural habitats "green" were more frequent than "bronze" ($p = 0.004$) ones (**Figure 4A**).

We observed no difference in female coloration between urban and rural regions (G = 0.65073, df = 2, $p = 0.722$). In urban regions, "green" dominated over "bronze" ($p = 0.002$) and "mixed" ($p = 0.003$) ones. In rural regions frequencies of "green" were higher than "bronze" ($p = 0.001$) ones (**Figure 4B**).

We found no changes in female coloration in rural regions over time (G = 6.0192, df = 4, $p = 0.198$). From 1892 to 1949 "green" ($p = 0.002$) and "mixed" ($p = 0.021$) dominated over "bronze" ones. From 1957 to 1998 "green" dominated over "bronze" ($p = 0.005$) and "mixed" ($p = 0.008$) ones. From 2016 to 2017 "green" were more frequent than "bronze" ($p < 0.001$) and "mixed" ($p = 0.002$) ones (**Figure 4C**).

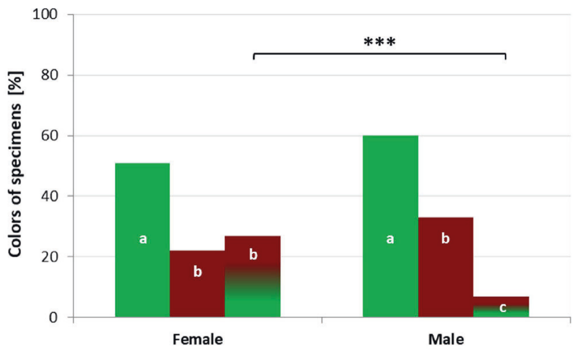

FIGURE 3 | Percentage of different color morphs in female and male *Harpalus affinis*; significant color differences between sexes are indicated by stars (***$p < 0.001$); significant differences between color morphs within a sex are indicated by differing letters.

In contrast, we observed significant differences in female coloration in urban regions over time (G = 42.03, df = 4, $p < 0.001$). This concerned comparisons between time periods from 1892 to 1949 and from 1957 to 1998 ($p < 0.001$), and from 1892 to 1949 and from 2016 to 2017 ($p < 0.001$). "Green" were more frequent from 2016 to 2017 than from 1892 to 1949 ($p < 0.013$). "Mixed" color frequencies remained constant across the three time periods. "Bronze" colors were more frequent from 1892 to 1949 than from 1957 to 1998 ($p < 0.001$) and from 2016 to 2017 ($p < 0.001$), but did not differ between 1957–1998 and 2016–2017 (**Figure 4D**).

In males we observed no coloration differences between urban, agricultural and near natural habitats (G = 7.532, df = 4, $p = 0.110$). However, in urban habitats "green" were more abundant than "bronze" ($p < 0.001$) and "mixed" ($p < 0.001$), and "bronze" were more frequent than "mixed" ($p < 0.001$) ones. In agricultural habitats the frequencies of "green" and "bronze" did not differ, but "green" ($p < 0.001$) and "bronze" ($p < 0.001$) were more abundant than "mixed" ones. In near natural habitats "green" were more frequent than "bronze" ($p < 0.001$) and "mixed" ($p < 0.001$), and "bronze" were more frequent than "mixed" ($p = 0.001$) ones (**Figure 5A**).

We observed no differences in male color morph composition between urban and rural regions (G = 0.98696, df = 2, $p = 0.912$). In urban regions "green" males were more frequent than "bronze" ($p = 0.025$) and "mixed" ($p < 0.001$) ones and "bronze" were more frequent than "mixed" ($p < 0.001$) ones. In rural regions the frequencies of "green" was higher than "bronze" ($p = 0.005$) and "mixed" ($p < 0.001$); and "bronze" were more frequent than "mixed" ($p < 0.001$) ones (**Figure 5B**).

No changes were found in male coloration in rural regions over time (G = 6.9052, df = 4, $p = 0.141$). From 1892 to 1949 frequencies of "green" and "bronze" did not differ, but both morphs were more frequent than "mixed" ($p < 0.001$) ones. From 1957 to 1998 "green" were more frequent than "bronze" ($p < 0.001$) and "mixed" ($p < 0.001$), and "bronze" were more

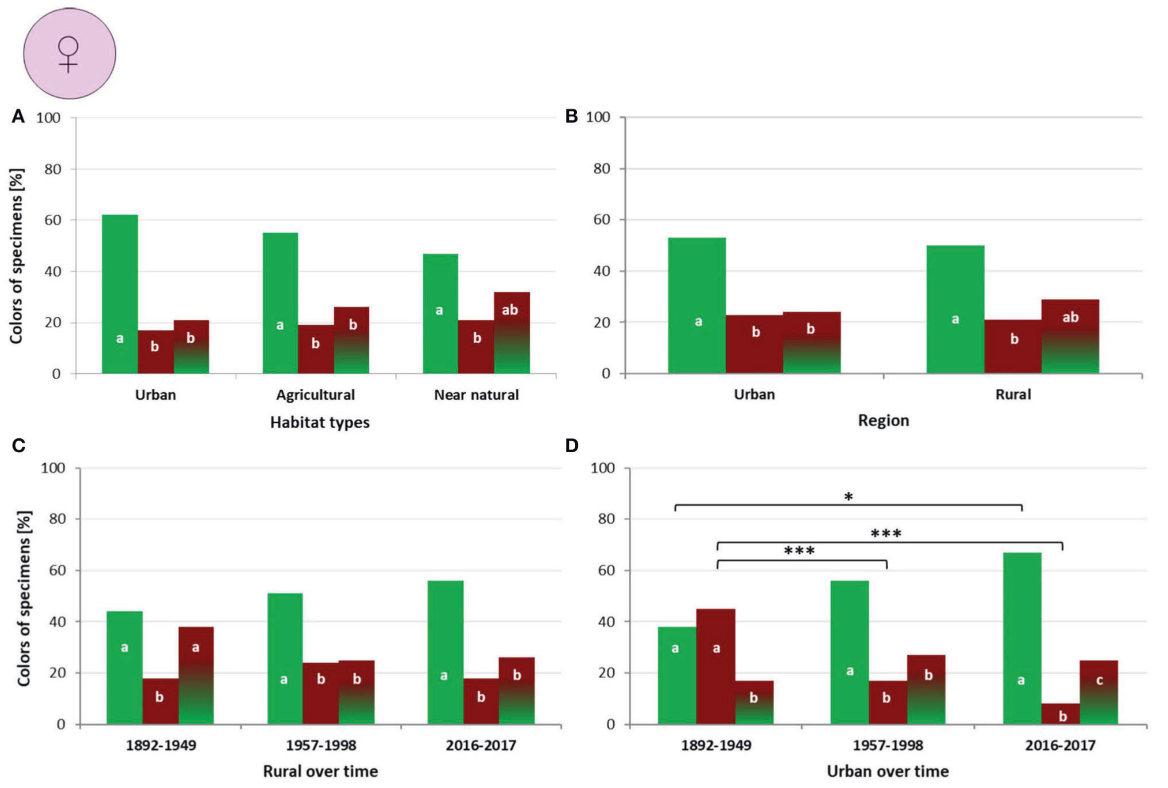

FIGURE 4 | Percentage of female *Harpalus affinis* color morphs in different habitat types **(A)**, regions with different urbanization level **(B)**, and within a particular region during different time periods **(C,D)**; different letters indicate significant differences in frequencies of the three color morphs; brackets with stars indicate significant difference between time periods (*$p < 0.05$; ***$p < 0.01$).

frequent than "mixed" ($p < 0.001$) ones. From 2016 to 2017 the frequencies of "green" and "bronze" did not differ, but both morphs were more frequent than "mixed" ($p < 0.001$) ones (**Figure 5C**).

We further observed no changes in male coloration in urban regions over time (G = 3.4427, df = 4, $p = 0.487$). From 1892 to 1949 the frequencies of "green" and "bronze" did not differ, but both were more frequent than "mixed" ($p < 0.001$) ones. From 1957 to 1998 "green" dominated over "bronze" ($p = 0.025$) and "mixed" ($p < 0.001$), and "bronze" were more frequent than "mixed" ($p < 0.001$). From 2016 to 2017 "green" dominated over "bronze" ($p = 0.030$) and "mixed" ($p < 0.001$), and "bronze" dominated over "mixed" ($p < 0.001$) ones (**Figure 5D**).

In summary frequencies of color morphs were different between sexes. The most frequent male color morph in males was "green," followed by "bronze," and "mixed." This pattern of color morph frequency was similar in every habitat, region and regions over time. In females the most frequent color morph was "green" as well, followed by "mixed" and "bronze." This applied to every habitat, region and in rural regions over time. However, in urban regions over time, frequencies of "bronze" morphs proportionally decreased, whereas the "green" morph increased over time.

DISCUSSION

Environmental alterations can lead to trait changes in species persisting in their altered habitats, and these changes can be observed across space and time (Van't Hof et al., 2011; Doudna and Danielson, 2015). Our study focused on changes in frequencies of color morphs in the diurnal ground beetle species *Harpalus affinis* in the Berlin-Brandenburg area, Germany, an area experiencing increasing urbanization and agriculture intensification during the last 125 years, with heavy air pollution in the early twentieth century due to industrialization, but with decreasing levels of air pollution after the Second World War (UBA, 1998). Generally, we observed that *H. affinis* displayed sexual color dimorphism. In females the frequencies of color morphs changed in urban regions over time, resulting in a decrease of "bronze," and an increase of "green" color morphs whereas color frequencies remained nearly constant in rural areas over time as well as between regions and habitats. In contrast, males were displaying no differences or changes in their color frequencies, neither in urban and rural regions over time, nor between regions and habitats. In general "green" was the main color morph in *H. affinis*. It was the most frequent color morph

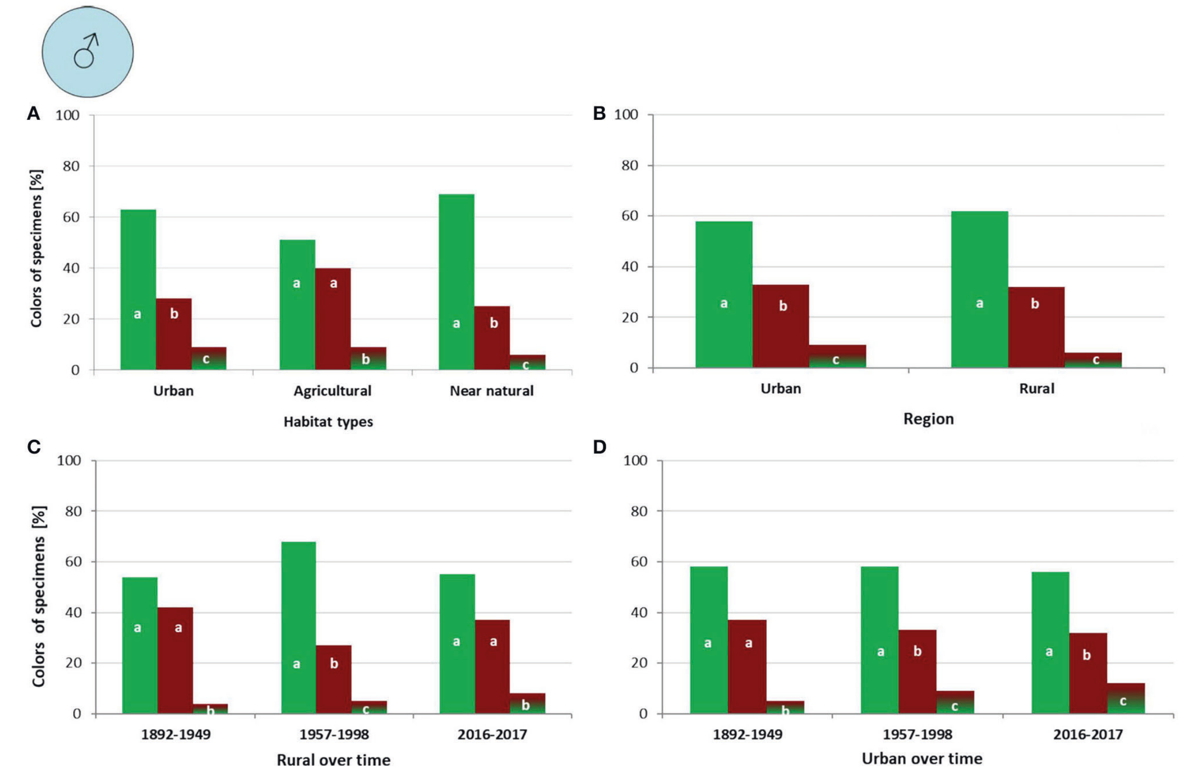

FIGURE 5 | Percentage of male *Harpalus affinis* color morphs in different habitat types **(A)**, regions with different urbanization level **(B)**, and within a particular region during different time periods **(C,D)**; different letters indicate significant differences in frequencies of the three color morphs.

in males in every observed habitat, region and regions over time as well as in females in habitats, regions, and rural regions over time. Generally, "green" is the most common multilayer color in beetles and has been hypothesized to have an important function in crypsis, e.g., to match substrates (Crowson, 1981; Parker, 1998). "Green" color seems to be the most advantageous color in a variety of habitats.

Although, "green" was shown to be the main color morph in *H. affinis*, in our first time period from 1892 to 1949, females in the city were more frequently "bronze" than "green." In the later time periods, 1957–1998 and 2016–2017, the frequencies of "bronze" decreased, whereas frequencies of "green" increased, becoming the most frequent color morph, as observed in males and rural females. The most likely explanation of this early urban deviation from the predominating color frequencies is habitat alternation in that time. The time from 1892 to 1949 was influenced by the effects of industrial revolution and the city of Berlin was affected by a high level of air pollution, especially by soot (Wey, 1982). In addition, Berlin rapidly expanded its urban space during that time period, resulting in rapid construction of buildings and streets (Buesch and Haus, 1987).

These changes might have resulted in natural selection for "bronze" color morphs. The selective advantage for a species to be polychromatic lies in the ability to be cryptic in different habitats: "Green" morphs in green environments are less visible for predators than other color morphs, living in the same habitat (Thiele, 1977).

However, in less green habitats like heath lands (Thiele, 1977) or habitats with less vegetation like urban environments, "bronze" color morphs may be better camouflaged than "green" ones. Birds are the main predators of ground beetles (Larochelle, 1980) and due to their excellent visual capabilities (Goldsmith, 2006) able to distinguish between both of the color morphs. This may have led to a selection for the "bronze," the least conspicuous, color morph in such soot polluted urban and vegetation-sparse habitats. Here the "bronze" beetles presumably were experiencing less predation pressure than "green" specimens (Thiele, 1977; Endler, 1988).

During the second time period, 1957–1998, first initiatives concerning environmental protection started (Pamme, 2003), and air pollution due to industrial soot commenced to decrease (UNEP/WHO, 1993; UBA, 1998), a process that continued until the most recent study period, 2016–2017 (SenStadtWohn, 2018). With decreasing pollution, "bronze" color morphs could have become again more conspicuous than the "green" morphs, the frequencies of both morphs consequently reversing over time.

Such fast changes in color frequencies due to predation pressure are well known in insect populations. Prominent examples concern environmental melanism (Harris, 1988), in the Two-spot Ladybird *Adila bipunctata* (Lusis, 1962; Creed, 1966), or the Peppered Moth, *Biston betularia*, the latter being a classic case of industrial melanism with reversions to whitish gray morphs, following reduction of air pollution (Kettlewell, 1955, 1956; Clarke and Sheppard, 1966; Bishop, 1972). Industrial melanism in polluted urban areas was observed in the twenties in England (Harrison and Garrett, 1926; Mokyr, 2010), a time period similar to our first time period and thus backing our interpretation of the predominant "bronze" colors in female beetles during that time.

In contrast, "green" remained the most frequent color morph in our first time period in rural regions, presumably less affected by construction works and pollution (Wey, 1982) so that "bronze" color morphs stayed more conspicuous and therefore more prone to predation in these regions, predominantly consisting of agricultural and near natural environments. Similar observations of color change in heavily air polluted regions only, changes being absent in less polluted regions, have been reported for *Biston betularia* by Bishop (1972). These findings are underlining our assumption that deviation in color frequencies in the first time period could be resulted due to effects of industrialization. Unfortunately, we do not have vouchers of *H. affinis*, predating 1892 in order to test if females of the Berlin population had been predominately "green" prior to urbanization. The dominance of that color morph in all other time periods and habitats however, is a strong argument for that assumption.

In contrast to females, we did not observe any habitat or time related changes in color frequencies in males, "green" always being the dominant color morphs. Although ecological and behavioral observations in beetles are comparatively rarely published (Seago et al., 2009), intraspecific differences in coloration suggests their potential role in intraspecific communication, like sexual signaling. Osawa and Nishida (1991) show that male elytral color is an important factor in female mate selection in the ladybird beetle *Harmonia axyridis*. Likewise, Arrow (1951) and Vulinec (1997) suggested that the iridescent surface of particular dung beetle males is preferred by females. Sexual selection by female choice could also be the reason for male *H. affinis* to remain predominantly "green," even in a polluted environment, if females more likely choose "green" males for mating. Then despite a higher predation risk males should remain "green" even in times with high levels of air pollution. Such tradeoff between mating success and survival is also described by Nokelainen et al. (2012) for the Wood Tiger Moth, *Parasemia plantaginis*: Here yellow color morphs provide better protection from predators due to aposematic coloration than the white morph. However, white males have higher mating success. In some birds, coloration has shown to be a signal of male quality (Hamilton and Zuk, 1982; Hill, 1991), and female mate choice is hypothesized to be an important selective driver toward brilliant colors in males (Darwin, 1874; Andersson, 1994; Hill, 2006). Similarly, other traits which should be eliminated by natural selection, are often favored by females' selection, like huge antlers or horns in various mammals or huge and elongated trails in peacocks (Darwin, 1874).

Due to limitation of the dataset and the sexual dichromatism found in *H. affinis*, specimens had to be divided into sexes before observing differences and changes in space and over time. This made sample sizes lower and influenced robustness of our findings. Alternative explanations for sex-specific differences in color adaptability in changing environments could be differences in behavior, different food preferences or living in different habitats. However, we have no hints that any of such differences exist and sexual dichromatism, found in *H. affinis*, is addition underlining our theory that sexual selection is the main driver of this effect.

CONCLUSIONS

In our study we could show a sexual dichromatism in *H. affinis* and we observed different, sex specific drivers for selection on color morphs. The appearance of "bronze" colored females during times of rapid urbanization and heavy environmental pollution is most likely due to natural selection. In contrast, males maintained their predominant "green" morph, presumably due to sexual selection. Further we could show that structural coloration is a useful trait for testing trait changes in species persisted in altered environments over space and time. Our results suggest that structural colorations may be able to change and reverse with changing environmental conditions within the relatively short time frame of 125 years or even less.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

SK, M-OR, JF, JM, and FM contributed conception and design of the study. JF organized the database. SK performed the statistical analysis and wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00525/full#supplementary-material

REFERENCES

Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Anjum-Zubair, M., Entling, M. H., Bruckner, A., Drapela, T., and Thomas, F. (2015). Differences of spring carabid beetle assemblages between semi-natural and adjoining winter wheat. *Agric. For. Entomol.* 17, 355–365. doi: 10.1111/afe.12115

Antrop, M. (2000). Changing patterns in the urbanized countryside of Western Europe. *Landsc. Ecol.* 15, 257–270. doi: 10.10/A:1008151109252

Antrop, M. (2004). Why landscapes of the past are important for the future. *Landsc. Urban Plan.* 70, 21–34. doi: 10.1016/j.landurbplan.2003.10.002

Arrow, G. J. (1951). Horned beetles: a study of the fantastic in nature. The Hague: W. Junk, Publishers.

Atkinson, D. (1994). Temperature and organism size: a biological law for ectotherms. *Adv. Ecol. Res.* 25, 1–58. doi: 10.1016/S0065-2504(08)60212-3

Bairoch, P., and Goertz, G. (1986). Factors of urbanisation in the nineteenth century developed countries: a descriptive and econometric analysis. *Urban Stud.* 23, 285–305. doi: 10.1080/00420988620080351

Bishop, J. A. (1972). An experimental study of the cline of industrial melanism in *Biston betularia* (L.) (Lepidoptera) between urban Liverpool and rural North Wales. *J. Anim. Ecol.* 41, 209–243. doi: 10.2307/3513

Brunk, I., and Wiegleb, G. (2006). Laufkäfer gestörter Landschaften der Niederlausitz-Bergbaufolgelandschaften. *Mitt. Dtsch. Ges. Allg. Angew. Entomol.* 15, 379–382.

Buesch, O., and Haus, W. (1987). *Berlin als Hauptstadt der Weimarer Republik 1919–1933*. New York, NY: Walter de Gruyter & Co. Berlin.

Cahan, S. H., Parker, D. J., Rissing, W. S., Johnson, A. R., Polony, S. T., Weiser, et al. (2002). Extreme genetic differences between queens and workers in hybridizing *Pogonomyrmex harvester* ants. *Proc. R. Soc. Lond.* 269, 1971–1877. doi: 10.1098/rspb.2002.2061

Clarke, C. A., and Sheppard, M. P. (1966). A local survey of the distribution of industrial melanic forms of the moths *Biston betularia* and estimates of the selective value of these in an industrial environment. *Proc. R. Soc. B.* 165, 424–439. doi: 10.1098/rspb.1966.0075

Cochrane, A., and Jonas, A. (1999). Reimagining Berlin: World city, national capital or ordinary place? *Eur. Urban Reg. Stud.* 6, 145–164. doi: 10.1177/096977649900600204

Cott, H. B. (1940). *Adaptive Coloration in Animals*. London: Methuen and Company.

Creed, E. R. (1966). Geographic variation in the Two-spot Ladybird in England and Wales. *Heredity* 21, 57–72. doi: 10.1038/hdy.1966.4

Crowson, R. (1981). *The Biology of the Coleoptera*. London: Academic Press.

Darwin, C. (1874). *The Descent of Man and Selection in Relation to Sex. 2nd Edn.* London: John Murray.

Deichsel, R. (2006). Species change in an urban setting - ground and rove beetles (Coleoptera: Carabidae and Staphylinidae) in Berlin. *Urban Ecosyst.* 9, 161–178. doi: 10.1007/s11252-006-8588-3

Doucet, S. M., and Hill, E. G. (2009). Do museum specimens accurately represent wild birds? A case study of carotenoid, melanin, and structural colours in long-tailed manakins *Chiroxiphia linearis*. *J. Avian Biol.* 40, 146–156. doi: 10.1111/j.1600-048X.2009.03763.x

Doudna, J. W., and Danielson, J. B. (2015). Rapid morphological change in the masticatory structures of an important ecosystem service provider. *PLoS ONE* 10:e0127218. doi: 10.1371/journal.pone.0127218

Endler, J. A. (1984). Progressive background matching in moths, a quantitative measure of crypsis. *Biol. J. Linn. Soc.* 22, 187–231. doi: 10.1111/j.1095-8312.1984.tb01677.x

Endler, J. A. (1988). Frequency-dependent predation, crypsis and aposematic coloration. *Philos. Trans. R. Soc. Lond. B.* 319, 505–523. doi: 10.1098/rstb.1988.0062

Erisman, J. W., Sutton, A. M., Galloway, J., Klimont, Z., and Winiwarter, W. (2008). How a century of ammonia synthesis changed the world. *Nat. Geosci.* 1, 636–639. doi: 10.1038/ngeo325

Forsman, A., and Shine, R. (1995). The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicate*. *Biol. J. Linn. Soc.* 55, 273–291. doi: 10.1111/j.1095-8312.1995.tb01066.x

Goldsmith, T. H. (2006). What birds see. *Sci. Am.* 295, 68–75. doi: 10.1038/scientificamerican0706-68

Hadley, N. F., Schultz, D. T., and Savill, A. (1988). Spectral reflectances of three subspecies of the tiger beetle *Neocicindela perhispida*: correlations with their respective habitat substrates. *N. Z. J. Zool.* 15, 343–346. doi: 10.1080/03014223.1988.10422624

Haila, Y. (2002). A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecol. Appl.* 12, 321–334. doi: 10.1890/1051-0761(2002)012[0321:ACGOFR]2.0.CO;2

Hamilton, D. W., and Zuk, W. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* 218, 384–387. doi: 10.1126/science.7123238

Harris, A. C. (1988). Cryptic colouration and melanism in the sand-burrowing beetle *Chaerodes trachyscelides* (Coleoptera: Tenebrionodae). *J. R. Soc. N. Z.* 18, 333–339. doi: 10.1080/03036758.1988.10426474

Harris, J. A., Hobbs, R. J., Higgs, E., and Aronson, J. (2006). Ecological restoration and global climate change. *Restor. Ecol.* 14, 170–176. doi: 10.1111/j.1526-100X.2006.00136.x

Harrison, J. W. H., and Garrett, F. C. (1926). The induction of melanism in the Lepidoptera and its subsequent inheritance. *Proc. R. Soc. Lond.* 99, 241–263. doi: 10.1098/rspb.1926.0012

Hervé, M. (2013). *Diverse Basic Statistical and Graphical Functions (RVAide Memoire)*. R Package. Available online at: https://CRAN.R-project.org/package=RVAideMemoire (accessed July 4, 2017).

Hill, G. E. (1991). Plumage coloration is a sexually selected indicator of male quality. *Nature* 350, 337–339. doi: 10.1038/350337a0

Hill, G. E. (2006). "Female choice for ornamental coloration," in *Bird Coloration, Function and Evolution*, Vol. 2, eds G. E. Hill and K. J. McGraw. Cambridge, MA: Harvard University Press.

Hobbs, R. J., Higgs, S. E., and Hall, C. (2013). *Novel Ecosystems: Intervening in the New Ecological World Order*. New York, NY: Wiley-Blackwell. doi: 10.1002/9781118354186

Jeltsch, F., Blaum, N., Brose, U., Chipperfield, D. J., Clough, Y., Farwig, N., et al. (2013). How can we bring together empiricists and modellers in functional biodiversity research? *Basic Appl. Ecol.* 14, 93–101. doi: 10.1016/j.baae.2013.01.001

Kenis, M., Auger-Rozenberg, A. M., Roques, A., and Timms, L. L. (2009). Ecological effects of invasive alien insects. *Biol. Invasions* 11, 21–45. doi: 10.1007/s10530-008-9318-y

Kettlewell, H. B. D. (1955). Selection experiments on industrial melanism in the Lepidoptera. *Heredity* 9, 323–342. doi: 10.1038/hdy.1955.36

Kettlewell, H. B. D. (1956). Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* 10, 287–301. doi: 10.1038/hdy.1956.28

Kinoshita, S., Yoshioka, S., and Miyazaki, J. (2008). Physics of structural colors. *Rep. Prog. Phys*. 71, 1–30. doi: 10.1088/0034-4885/71/7/076401

Kraetke, S. (2000). Berlin: the metropolis as a production space. *Eur. Plan. Stud*. 8, 7–27. doi: 10.1080/096543100110901

Land, M. F. (1972). The physics and biology of animal reflectors. *Progr. Biophys. Mol. Biol*. 24, 75–106. doi: 10.1016/0079-6107(72)90004-1

Larochelle, A. (1980). A list of birds of Europe and Asia as predators of carabid beetles including Cicindelini (Coleoptera: Carabidae). *Cordulia* 6, 1–19.

Loevei, G. L., and McCambridge, M. (2002). Adult mortality and minimum lifespan of the ground beetle *Harpalus affinis* (Coleoptera: Carabidae) in New Zealand. *N. Z. J. Zool*. 29, 1–4. doi: 10.1080/03014223.2002.9518283

Lusis, J. J. (1962). On the biological meaning of colour polymorphism of lady beetle *Adalia bipunctata* L. Izv. Byuro Genet. *Leningrad* 6, 89–163.

Maas, S., Detzel, P., and Staudt, A. (2002*). Gefährdungsanalyse der Heuschrecken Deutschlands - Verbreitungsatlas, Gefährdungseinstufung und Schutzkonzepte.* Münster-Hiltru: Bundesamt für Naturschutz; Landwirtschaftsverlag.

McCabe, J., and Patridge, L. (1997). An interaction between environmental temperature and genetic variation for body size for the fitness of adult female *Drosophila melanogaster*. *Evolution* 51, 1164–1174. doi: 10.1111/j.1558-5646.1997.tb03964.x

Mokyr, J. (2010). *The Enlightened Economy an Economic History of Britain 1700–1850*. New Haven, CT: Yale University Press.

Nokelainen, O., Hegna, H. R., Reudler, J. H., Lindstedt, C., and Mappes, J. (2012). Trade-off between warning signal efficacy and mating success in the wood tiger moth. *Proc. R. Soc. B*. 279, 257–265. doi: 10.1098/rspb.2011.0880

Noyes, J. A., Vukusic, P., and Hooper, I. R. (2007). Experimental method for reliably establishing the refractive index of buprestid beetle exocuticle. *Opt. Express* 15, 4351–4358. doi: 10.1364/OE.15.004351

Osawa, N., and Nishida, T. (1991). Seasonal variation in elytral colour polymorphism in *Harmonia axyridis* (the ladybird beetle): the role of non-random mating. *Heredity* 69, 297–307. doi: 10.1038/hdy.1992.129

Palkovacs, E. P., Kinnison, T. M., Correa, C., Dalton, M. C., and Hendry, P. A. (2011). Fates beyond traits: ecological consequences of human-induced trait change. *Evol. Appl*. 5, 183–191. doi: 10.1111/j.1752-4571.2011.00212.x

Palmer, R. A., and Strobeck, C. (1992). Fluctuating asymmetry as a measure of developmental stability: Implications of non-normal distributions and power of statistical traits. Acta Zool. *Fenn*. 191, 57–72.

Pamme, H. (2003). "Das Politikfeld Umweltpolitik," in *Verwaltungshandeln in Politikfeldern,* ed D. Grunow (Opladen: Leske and Budrich), 185–224.

Parker, A. (1998). The diversity and implications of animal structural colours. *J. Exp. Biol*. 201, 2343–2347.

Parker, A. R., and McKenzie, D. (2003). The cause of 50 million year-old colour. *Proc. R. Soc. B*. 270, 151–153. doi: 10.1098/rsbl,.2003.0055

R Core Team (2017). *R: A Language and Environment Statistical Computing.* Vienna: R Foundation for Statistical Computing. Available online at: http://www.R-project.org/ (accessed July 4, 2018).

Ribbe, W., Bohm, E., Schich, W., and Schulz, K. (2002a). *Geschichte Berlins. Band 1: Von der Frühgeschichte bis zur Industrialisierung*. München: Beck.

Ribbe, W., Bohm, E., Schich, W., and Schulz, K. (2002b). *Geschichte Berlins. Band 2: Von der Märzrevolution bis zur Gegenwart*. München: Beck.

Ribera, I., Dolédec, S., Dowmie, S. I., and Foster, N. G. (2001). Effects of land disturbance and stress on species traits of ground beetle assemblages. *Ecology* 82, 1112–1129. doi: 10.1890/0012-9658(2001)082[1112:EOLDAS]2.0.CO;2

Ricciardi, A. (2007). Are modern biological invasions an unprecedented form of global change? *Conserv. Biol*. 21, 329–336. doi: 10.1111/j.1523-1739.2006.00615.x

Rocha, L. A., Aleixo, A., Allen, G., Almeda, F., Baldwin, C. C., Barclay, L. V. M., et al. (2014). Specimen collection: an essential tool. *Science* 344, 814–815. doi: 10.1126/science.344.6186.814

Root, T. L., and Schneider, H. S. (2006). Conservation and climate change: the challenges ahead. *Conserv. Biol*. 20, 706–708. doi: 10.1111/j.1523-1739.2006.00465.x

Schildt, A., and Sywottek, A. (1993). *Modernisierung im Wiederaufbau. - Die westdeutsche Gesellschafft der 50er Jahre*. Bonn: Verlag J. H. W. Dietz.

Schultz, T. D., and Rankin, A. M. (1985). Developmental changes in the interference reflectors and colorations of tiger beetles (Cicindela). *J. Exp. Biol*. 117, 111–118.

Seago, A. E., Brady, P., Vigneron, J., and Schultz, D. (2009). Gold bugs and beyond: a review of iridescence and structural colour mechanisms in beetles (Coleoptera). *J. R. Sock. Interface* 6, 165–184. doi: 10.1098/rsif.2008.0354.focus

SenStadtWohn (Senatsverwaltung für Stadtentwicklung und Wohnen Berlin) (2018). *Langjährige Entwicklung der Luftqualität*. Available online at: https://www.stadtentwicklung.berlin.de/umwelt/umweltatlas/d312_03.htm (accessed September18, 2019).

Storfer, A., Cross, J., Rush, V., and Caruso, J. (1999). Adaptive coloration and gene flow as a constraint to local adaptation in the streamside salamander, *Ambystoma barbouri*. *Evolution* 53, 889–898. doi: 10.1111/j.1558-5646.1999.tb05383.x

Sunderland, K. D., Loevei, L. G., and Fenlon, J. (1995). Diets and reproductive phenologies of the introduced ground beetles *Harpalus affinis* and *Cilvina australasiae* (Coleoptera: Carabidae) in New Zealand. *Aust. J. Zool*. 43, 39–50. doi: 10.1071/ZO9950039

Sustek, Z. (1992). Changes in representation of carabid life forms along an urbanization gradient (Coleoptera, Carabidae). *Biol. Brat*. 47, 417–430.

Thiele, H.-U. (1977). *Carabid Beetles in Their Environments.* Berlin; Heidelberg; New York: Springer.

Tilman, D., Cassman, K. G., Matson, A. P., Naylor, R., and Polasky, S. (2002). Agricultural sustainability and intensive production practices. *Nature* 418, 671–677. doi: 10.1038/nature01014

Townsend, J. I. (1992). *Harpalus affinis* (Schrank) (Coleoptera: Carabidae) recently established in the North Island of New Zealand. *N. Z. Entomol*. 15, 25–29. doi: 10.1080/00779962.1992.9722624

Tyler, G. (2010). Variability in colour, metallic luster, and body size of *Carabus arvensis* Herbst, 1784 (Coleoptera: Carabidae) in relation to habitat properties. *Entomol. Fenn*. 21, 90–96. doi: 10.33338/ef.84514

UBA (1998). *Umweltdaten Deutschland*. Berlin: Umweltbundesamt; Erich Schmidt Verlag.

UNEP/WHO (1993). *City Air Quality Trends*, Vol. 2. WHO PEP/93 26, UNE93 26P GEMS 93.A.2, Genf.

United Nations (2002). *World Population Prospects: The 2001 Revision. Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat*.

Van't Hof, A., Edmonds, E., Dalikova, M., Marec, F., and Saccheri, J. I. (2011). Industrial melanism in British Peppered Moths has a singular and recent mutational origin. *Science*. 332, 958–960. doi: 10.1126/science.1203043

Vulinec, K. (1997). Iridescent dung beetles: a different angle. *Fla. Entomol*. 80, 132–141. doi: 10.2307/3495550

Wey, K.-G. (1982). *Umweltpolitik in Deutschland. Kurze Geschichte des Umweltschutzes in Deutschland seit 1900*. Opladen: Westdeutscher Verlag.

Wrase, D. W. (2004). "Harpalina," in *Die Käfer Mitteleuropas: Adephaga 1: Carabidae (Laufkäfer),* eds H. Freude, K. W. Harde, G. A. Lohse, B. Klausberger, and G. Müller-Motzfeld (Heidelberg; Berlin: Spektrum-Verlag).

Ziegler, J. (2011). Rezente Arealerweiterungen bei Wanzenfliegen (Diptera: Tachinidae, Phasiinae) in Nordostdeutschland und eine Übersicht zur Gesamtverbreitung von fünf Arten. *Stud. Dipterol*. 18, 29–54.

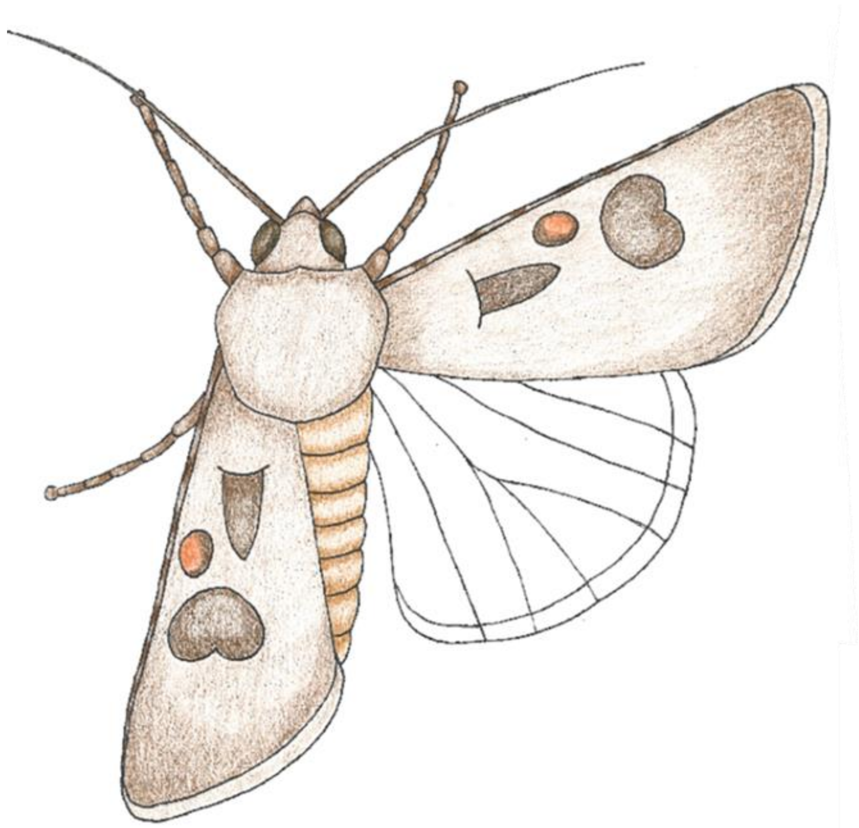
Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

6. Supplementary material

6.1 Supplementary material: Paper 1

Impact of light pollution on moth morphology – a 137-year study in Germany

Keinath, S., Hölker, F., Müller, J., & Rödel, M.-O. (2021). *Impact of light pollution on moth morphology – a 137-year study in Germany.* Basic and Applied Ecology - Urban ecosystems – their potentials, challenges and solutions. https://doi.org/10.1016/j.baae.2021.05.004



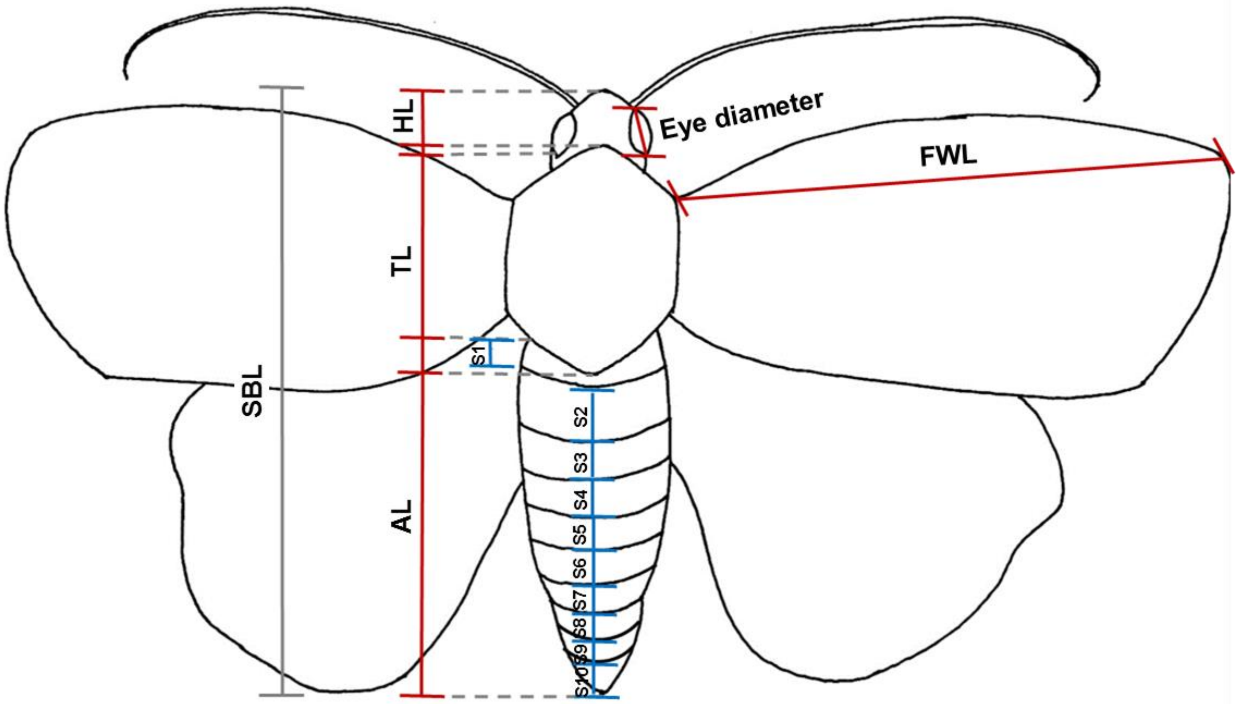


Figure A Different morphological measures taken from *Agrotis exclamationis*: Standardized body size (SBL) comprising head length (HL), tibia length (TL), and abdominal length (AL). For the latter we summed up all single segment measures (S1-10); horizontal diameter of eyes (eyes diameter), and forewing length (FWL).

Table 1B Temporal effects of Radiance, Year, their interaction and Sex on *Agrotis exclamationis*'. Standardized body size (SBL); Mean diameter of the right and left eyes in ratio to SBL (eye diameter / SBL); and mean lengths of the right and left forewing in ratio to SBL (FWL / SBL). Linear models were used. Significant p-values are given in bold.

Dependent variable	Independent variable	df	t-value	p-value
SBL	Radiance	74	-0.840	0.959
	Year	74	2.402	**0.019**
	Sex	74	-4.070	**<0.001**
	Radiance * Year	74	0.961	0.340
Eye diameter / SBL	Radiance	74	0.538	0.592
	Year	74	-2.474	**0.016**
	Sex	74	7.757	**<0.001**
	Radiance * Year	74	-0.521	0.603
FWL / SBL	Radiance	73	0.581	0.563
	Year	73	-1.821	0.073
	Sex	73	-0.351	0.727
	Radiance * Year	73	-0.576	0.566

Table 2B Temporal effects of Light Pollution Categories (LPC), Year, their interaction and Sex on *Agrotis exclamationis*' Standardized body size (SBL); Mean diameter of the right and left eyes in ratio to SBL (eye diameter / SBL); and mean lengths of the right and left forewing in ratio to SBL (FWL / SBL). Linear models were used. Significant p-values are given in bold; nearly significant p-values, showing a trend, are marked in grey.

Dependent variable	Independent variable	df	t-value	p-value
SBL	LPC	74	0.171	0.581
	Year	74	1.486	0.141
	Sex	74	-4.214	**<0.001**
	LPC * Year	74	0.202	0.841
Eye diameter/ SBL	LPC	74	-1.949	0.055
	Year	74	-3.034	**<0.010**
	Sex	74	8.227	**<0.001**
	LPC * Year	74	1.988	0.051
FWL / SBL	LPC	73	-0.813	0.419
	Year	73	-1.884	0.064
	Sex	73	-0.094	0.926
	LPC * Year	73	0.857	0.394

Table 3B Spatial effects of Light Pollution Categories (LPC) on *Agrotis exclamationis*‘ sexes. Standardized body size (SBL); Mean diameter of the right and left eyes in ratio to SBL (eye diameter / SBL); and mean lengths of the right and left forewing in ratio to SBL (FWL / SBL). Analyses of variance (ANOVA) were used.

Dependent variable	Grouping variable	Sex	df	F-value	p-value
SBL	LPC	male	2	0.479	0.625
		female	2	1.337	0.273
Eye diameter / SBL	LPC	male	2	0.387	0.676
		female	2	1.842	0.170
FWL / SBL	LPC	male	2	0.012	0.988
		female	2	0.451	0.640

Table 1C Sample areas within Berlin or Brandenburg of *Agrotis exclamationis* specimens with sex (f = female; m = male), districts, sampling year, GPS coordinates (latitude; longitude), Rate of light pollution change over 7 years in %, Radiance values in 10-9 W / cm2 * sr, light pollution categories (LPC), measurements of standardized body size in mm (SBL), mean diameter of right and left eyes in relation to SBL (Dia eyes / SBL), and mean length of right and left forewings (FWL / SBL).

ID	Region	Sex	District	Year	Latitude	Longitude	Rate of change	Radiance	LPC	SBL	Dia eyes/SBL	FWL/SBL
1	Berlin	f	Berlin	1885	52,52233	13,40553	24,89	0,61	medium	19,12	0,122	0,881
2	Berlin	f	Spandau	1901	52,5349	13,20225	1,51	21,01	high	18,32	0,128	0,860
3	Berlin	f	Spandau	1901	52,5349	13,20225	1,51	21,01	high	18,60	0,122	0,855
4	Berlin	f	Berlin Friedrichsfelde	1973	52,51403	13,45403	11,61	11,77	high	19,94	0,113	0,820
5	Berlin	f	Kladow in Spandau	1973	52,45305	13,1426	7,96	3,83	high	20,00	0,115	0,863
6	Berlin	f	Kladow in Spandau	1973	52,45305	13,1426	7,96	3,83	high	17,54	0,133	0,881
7	Berlin	f	Tierpark Berlin	1974	52,50261	13,53099	5,81	8,22	high	17,76	0,114	0,859
8	Berlin	f	Spandauer Forst West	2017	52,4435	13,50203	no	1,46	medium	20,16	0,112	0,809
9	Berlin	f	Gewerbegebiet Nähe Flughafen Johannisthal	2017	52,4144	13,09478	no	14,83	high	18,76	0,127	0,869
10	Berlin	f	Glienicker Volkspark, Wannsee	2017	52,4144	13,09478	no	6,28	high	19,84	0,116	0,759
11	Berlin	f	Glienicker Volkspark, Wannsee	2017	52,49318	13,28564	no	6,28	high	20,40	0,105	0,794
12	Berlin	f	Grunewald-Süd	2017	52,49318	13,28564	no	21,22	high	20,42	0,115	0,847
13	Berlin	f	Grunewald-Süd	2017	52,50323	13,58062	no	21,22	high	19,78	0,118	0,854
14	Berlin	f	Kaulsdorf	2017	52,45824	13,49718	no	16,96	high	21,38	0,113	0,692
15	Berlin	f	Königsheide/Kanal	2017	52,53551	13,3841	no	13,98	high	19,56	0,118	0,826
16	Berlin	f	Nordbahnhof	2017	52,53551	13,3841	no	30,93	high	22,50	0,102	0,758
17	Berlin	f	Nordbahnhof	2017	52,57234	13,15864	no	30,93	high	21,18	0,109	0,744
18	Berlin	f	Tegeler See	2017	52,56864	13,25664	no	2,28	high	20,70	0,111	0,838
19	Berlin	f	Tegeler See	2017	52,56864	13,25664	no	2,28	high	20,76	0,119	0,819
20	Berlin	f	Tegeler See	2017	52,56864	13,25664	no	2,28	high	19,94	0,109	0,803
21	Berlin	f	Tiergarten	2017	52,51750	13,36482	no	42,43	high	19,38	0,111	0,906
22	Berlin	f	Tiergarten	2017	52,51750	13,36482	no	42,43	high	20,48	0,112	0,789
23	Berlin	f	Tiergarten	2017	52,51750	13,36482	no	42,43	high	20,56	0,118	0,737
24	Berlin	f	Tiergarten	2017	52,51750	13,36482	no	42,43	high	19,74	0,115	0,816
25	Berlin	m	Berlin	1880	52,52233	13,40553	24,89	0,50	medium	15,90	0,145	0,972

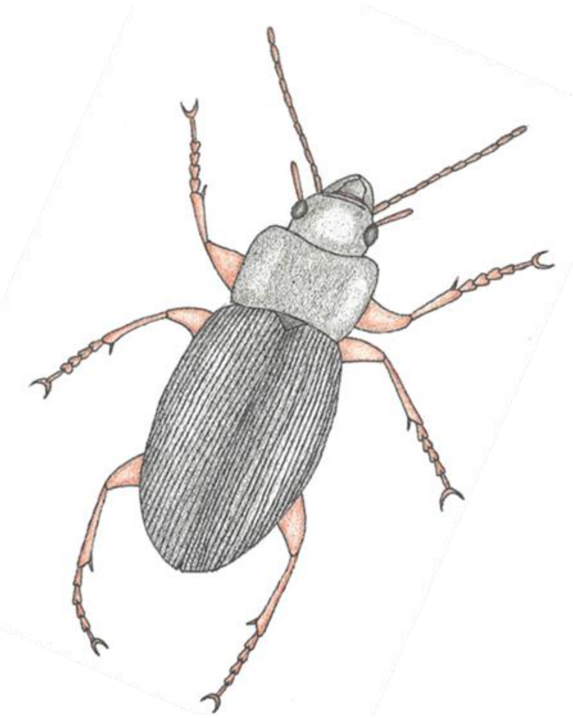
ID	Region	Sex	District	Year	Latitude	Longitude	Rate of change	Radiance	LPC	SBL	Dia eyes/SBL	FWL/SBL
26	Berlin	m	Buch	1960	52,63428	13,49757	2,96	10,74	high	15,50	0,159	1,003
27	Berlin	m	Kladow in Spandau	1973	52,45305	13,1426	7,96	3,83	high	17,88	0,138	0,875
28	Berlin	m	Pfaueninsel	1974	52,43461	13,12921	27,94	0,14	low	16,36	0,155	0,987
29	Berlin	m	Rosenthal	1975	52,59985	13,37776	5,36	7,12	high	18,44	0,131	0,767
30	Berlin	m	Rosenthal	1975	52,59985	13,37776	5,36	7,12	high	17,68	0,128	0,860
31	Berlin	m	Jungfernheide	2010	52,56416	13,26363	14,18	3,57	high	15,06	0,150	0,936
32	Berlin	m	Jungfernheide	2010	52,56416	13,26363	14,18	3,57	high	15,88	0,152	0,904
33	Berlin	m	Spandauer Forst	2017	52,4435	13,50203	no	1,46	medium	21,54	0,118	0,787
34	Berlin	m	Gewerbegebiet Nähe Flughafen Johannisthal	2017	52,45824	13,49718	no	14,83	high	21,50	0,129	0,721
35	Berlin	m	Königsheide/Kanal	2017	52,45824	13,49718	no	13,98	high	20,18	0,120	0,768
36	Berlin	m	Königsheide/Kanal	2017	52,53551	13,3841	no	13,98	high	19,60	0,124	NA
37	Berlin	m	Nordbahnhof	2017	52,47835	13,35606	no	30,93	high	19,60	0,132	0,793
38	Berlin	m	Sachsendamm, Schöneberg	2017	52,57234	13,15864	no	41,44	high	19,10	0,135	0,770
39	Brandenburg	f	Heiligengrabe	1898	53,14473	12,36269	25,56	0,01	low	19,52	0,112	0,799
40	Brandenburg	f	Heiligengrabe	1898	53,14473	12,36269	25,56	0,01	low	19,42	0,116	0,834
41	Brandenburg	f	Heiligengrabe	1898	53,14473	12,36269	25,56	0,01	low	18,94	0,115	0,834
42	Brandenburg	f	Heiligengrabe	1898	53,14473	12,36269	25,56	0,01	low	17,94	0,135	0,858
43	Brandenburg	f	Heiligengrabe	1898	53,14473	12,36269	25,56	0,01	low	19,58	0,126	0,820
44	Brandenburg	f	Eiche (Potsdam)	1905	52,40503	12,99271	13,51	0,79	medium	21,94	0,107	0,802
45	Brandenburg	f	Eiche (Potsdam)	1905	52,40503	12,99271	13,51	0,79	medium	18,62	0,113	0,857
46	Brandenburg	f	Finkenkrug	1918	52,55976	13,07448	15,64	0,69	medium	21,40	0,108	0,722
47	Brandenburg	f	Finkenkrug	1919	52,55976	13,07448	15,64	0,71	medium	16,90	0,129	0,899
48	Brandenburg	f	Zehdenick	1946	52,97786	13,33121	11,37	1,96	high	19,82	0,106	0,827
49	Brandenburg	f	Zehdenick	1950	52,97786	13,33121	11,37	1,86	high	17,64	0,119	0,867
50	Brandenburg	f	Zehdenick	1957	52,97786	13,33121	11,37	2,29	high	19,12	0,120	0,860
51	Brandenburg	f	Hennigsdorf	1958	52,63401	13,20651	13,69	5,67	high	18,00	0,130	0,950
52	Brandenburg	f	Hennigsdorf	1958	52,63401	13,20651	13,69	5,67	high	18,48	0,122	0,904
53	Brandenburg	f	Gransee (Oberhavel)	1960	53,00693	13,15042	15,26	0,67	medium	19,52	0,118	0,830
54	Brandenburg	f	Sommerfeld (Kremmen) Kreis Oranienburg	1971	52,80298	13,03195	2,98	1,40	medium	22,54	0,106	0,756
55	Brandenburg	f	Schlepzig (Cottbus)	1974	52,02854	13,89379	12,98	0,54	medium	22,52	0,100	0,731

ID	Region	Sex	District	Year	Latitude	Longitude	Rate of change	Radiance	LPC	SBL	Dia eyes/SBL	FWL/SBL
56	Brandenburg	f	Nauen	1976	52,60918	12,87953	6,77	9,12	high	22,14	0,111	0,800
57	Brandenburg	f	Nauen	1976	52,60918	12,87953	6,77	9,12	high	19,60	0,109	0,809
58	Brandenburg	f	Schöneweide	1982	52,10779	13,27186	28,51	0,22	medium	19,00	0,109	0,800
59	Brandenburg	f	Körba	1983	51,80676	13,39198	28,92	0,12	low	19,38	0,121	0,833
60	Brandenburg	f	Tornow	1998	53,06463	13,28744	36,52	0,08	low	18,90	0,113	0,809
61	Brandenburg	f	Dreilinden	2017	52,40414	13,17177	no	4,00	high	20,50	0,110	0,839
62	Brandenburg	f	Dreilinden	2017	52,40414	13,17177	no	4,00	high	21,16	0,105	0,775
63	Brandenburg	m	Heiligengrabe	1898	53,14482	12,36239	25,56	0,01	low	17,36	0,142	0,916
64	Brandenburg	m	Heiligengrabe	1898	53,14482	12,36239	25,56	0,01	low	15,28	0,151	0,995
65	Brandenburg	m	Heiligengrabe	1898	53,14482	12,36239	25,56	0,01	low	19,18	0,134	0,813
66	Brandenburg	m	Heiligengrabe	1898	53,14482	12,36239	25,56	0,01	low	18,26	0,133	0,767
67	Brandenburg	m	Heiligengrabe	1898	53,14482	12,36239	25,56	0,01	low	16,94	0,148	0,838
68	Brandenburg	m	Potsdam	1913	52,39960	13,04782	6,21	11,04	high	18,28	0,128	0,845
69	Brandenburg	m	Stahnsdorf	1929	52,39199	13,22175	11,41	1,97	high	19,68	0,121	0,803
70	Brandenburg	m	Zehdenick Stadt	1952	52,97786	13,33121	11,37	2,18	high	18,36	0,132	0,861
71	Brandenburg	m	Hennigsdorf	1958	52,63402	13,20647	13,69	5,67	high	18,08	0,136	0,841
72	Brandenburg	m	Rüdersdorf	1958	52,47176	13,78511	7,38	3,21	high	18,30	0,130	0,817
73	Brandenburg	m	Rüdersdorf	1958	52,47176	13,78511	7,38	3,21	high	18,40	0,138	0,560
74	Brandenburg	m	Sommerfeld (Kremmen) Kreis Oranienburg	1968	52,80298	13,03195	2,98	1,39	medium	19,46	0,133	0,804
75	Brandenburg	m	Umgebung Rathenow	1970	52,80298	13,03195	26,7	0,06	low	20,47	0,110	0,725
76	Brandenburg	m	Sommerfeld (Kremmen) Kreis Oranienburg	1970	52,61659	12,32470	2,98	1,40	medium	17,78	0,132	0,835
77	Brandenburg	m	Güldenhof und Umgebung (Kreis Gransee)	1987	53,08275	13,05445	51,13	0,01	low	19,90	0,114	0,503
78	Brandenburg	m	Nedlitz	1988	52,44008	13,03487	26,7	0,81	medium	20,32	0,115	0,726
79	Brandenburg	m	Umgebung Rathenow	1989	52,61659	12,32470	26,7	0,14	low	18,60	0,115	0,793

6.2 Supplementary material: Paper 2

Body sizes and dietary niche of two ground beetle species from urban and rural populations, tracked from 1900 to today

Keinath, S., Frisch, J., Müller, J., Mayer, F., Struck, U., & Rödel, M.-O. *Body sizes and dietary niche of two ground beetle species from urban and rural populations, tracked from 1900 to today.*



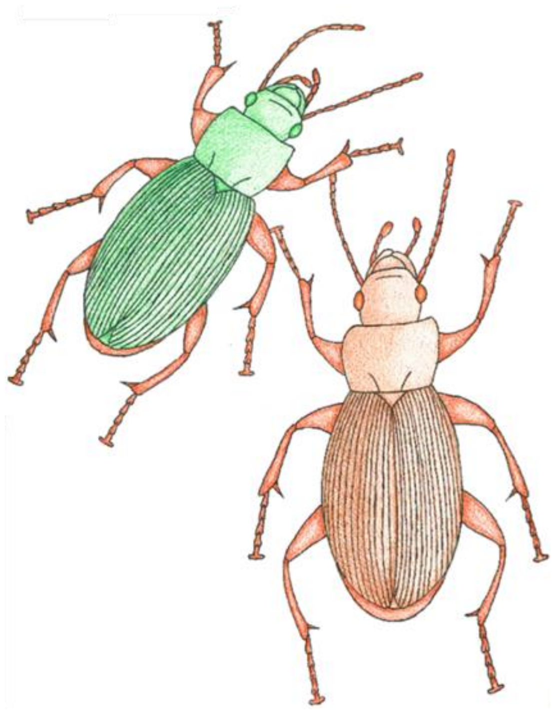


Table A1 Body lengths (in mm) of *Harpalus affinis* and *H. rufipes* from agricultural and urban habitats, rural and city areas across space and time per sex: Results of Wilcoxon rank sum tests (Wilcox.) for comparisons of body lengths between females and males, for comparisons of body lengths between habitats in females and males, and for comparisons of body lengths between areas in females and males. Results of Kruskal-Wallis rank sum tests (Krusk.-Wal.) for comparisons of body lengths between time periods in rural areas in females and males, and between time periods in city areas in females and males, significant differences are given in bold.

Species	Comparison	Sex	Medians [mm]		Test	w-value	chi-square	p-value
H. affinis	SBL ~ Sex	-	female	9.01	Wilcox.	63318	-	**< 0.0001**
			male	8.70				
	SBL ~ Habitat	female	agricultural	9.22	Wilcox.	78.5	-	0.728
			urban	8.88				
		male	agricultural	8.51		170.5	-	0.229
			urban	8.70				
	SBL ~ Area	female	rural	9.07	Wilcox.	7468.5	-	0.780
			city	9.01				
		male	rural	8.76		19296	-	0.313
			city	8.63				
	SBL ~ Rural over time	female	1892-1949	8.88	Krusk.-Wal.	-	0.3305	0.848
			1957-1998	9.07				
			2016-2017	9.22				
		male	1892-1949	8.76		-	1.0705	0.586
			1957-1998	8.76				
			2016-2017	8.51				
	SBL ~ City over time	female	1892-1949	9.09	Krusk.-Wal.	-	2.0146	0.365
			1957-1998	9.01				
			2016-2017	8.88				
		male	1892-1949	8.62		-	1.1425	0.565
			1957-1998	8.63				
			2016-2017	8.70				
H. rufipes	SBL ~ Sex	-	female	13.46	Wilcox.	6557	-	**< 0.0001**
			male	12.53				
	SBL ~ Habitat	female	agricultural	13.52	Wilcox.	272	-	0.142
			urban	13.17				
		male	agricultural	12.64		298	-	0.081
			urban	12.15				
	SBL ~ Area	female	rural	13.52	Wilcox.	775	-	0.196
			city	13.17				
		male	rural	12.52		1046.5	-	0.587
			city	12.57				
	SBL ~ Rural over time	female	1892-1949	13.22	Krusk.-Wal.	-	1.9911	0.370
			1957-1998	13.64				
			2016-2017	13.52				
		male	1892-1949	12.38		-	2.3087	0.315
			1957-1998	12.29				
			2016-2017	12.64				
	SBL ~ City over time	female	1892-1949	12.96	Krusk.-Wal.	-	0.76896	0.681
			1957-1998	13.64				
			2016-2017	12.87				
		male	1892-1949	12.93		-	10.516	**0.005**
			1957-1998	13.09				
			2016-2017	11.76				

Table A2 Body lengths (in mm) of *Harpalus affinis* and *H. rufipes* from agricultural and urban habitats, rural and city areas across space and time per sex: Results of Levene´s Test for Homogeneity of Variance, centre = median. Significant p-values are given in bold.

Species	Comparison	Sex	Medians		Df	F-value	p-value
H. affinis	SBL ~ Habitat	female	agricultural	0.357	22	1.559	0.225
			urban	0.177			
		male	agricultural	0.268	40	1.694	0.201
			urban	1.212			
	SBL ~ Area	female	rural	0.399	240	1.538	0.249
			city	0.355			
		male	rural	0.251	380	1.887	0.170
			city	0.444			
	SBL ~ Rural over time	female	1892-1949	0.5745	121	0.829	0.439
			1957-1998	0.322			
			2016-2017	0.357			
		male	1892-1949	0.189	196	0.488	0.615
			1957-1998	0.275			
			2016-2017	0.268			
	SBL ~ City over time	female	1892-1949	0.336	115	0.273	0.762
			1957-1998	0.389			
			2016-2017	0.195			
		male	1892-1949	0.192	180	4.010	**0.020**
			1957-1998	0.394			
			2016-2017	1.368			
H. rufipes	SBL ~ Habitat	female	agricultural	0.366	53	0.281	0.598
			urban	0.229			
		male	agricultural	0.364	43	5.391	**0.025**
			urban	0.884			
	SBL ~ Area	female	rural	0.399	240	1.338	0.249
			city	0.355			
		male	rural	0.434	94	5.157	**0.025**
			city	0.764			
	SBL ~ Rural over time	female	1892-1949	0.720	59	1.279	0.286
			1957-1998	0.882			
			2016-2017	0.366			
		male	1892-1949	0.525	52	0.543	0.584
			1957-1998	0.526			
			2016-2017	0.364			
	SBL ~ City over time	female	1892-1949	0.664	18	1.072	0.363
			1957-1998	3.196			
			2016-2017	0.269			
		male	1892-1949	0.635	37	0.413	0.665
			1957-1998	0.317			
			2016-2017	0.662			

Table A3 Stable ^{14}N and ^{13}C isotope enrichments (in %) in cuticula, legs, and muscles of *Harpalus affinis* and *H. rufipes* between sexes and specimens from agricultural and urban habitats. Results of Wilcoxon rank sum tests for comparisons between tissues of females and males and between beetles originated from agricultural and urban habitats. Significant differences are given in bold.

Species	Tissue	Comparison	Medians		w-value	p-value
H. affinis	**Cuticula**	$\delta\ ^{15}N$ ~ Sex	female	5.816	66	0.248
			male	3.082		
		$\delta\ ^{13}C$ ~ Sex	female	-26.656	40.5	0.496
			male	-26.134		
		$\delta\ ^{15}N$ ~ Habitat	agricultural	6.283	85	**0.007**
			urban	2.839		
		$\delta\ ^{13}C$ ~ Habitat	agricultural	-26.389	40.5	0.496
			urban	-26.311		
	Legs	$\delta\ ^{15}N$ ~ Sex	female	5.601	63	0.353
			male	3.177		
		$\delta\ ^{13}C$ ~ Sex	female	-26.426	46	0.796
			male	-26.289		
		$\delta\ ^{15}N$ ~ Habitat	agriculture	6.3840	89	**0.002**
			urban	2.9185		
		$\delta\ ^{13}C$ ~ Habitat	agricultural	-26.301	49	0.971
			urban	-26.313		
	Muscles	$\delta\ ^{15}N$ ~ Sex	female	6.754	24	0.622
			male	5.310		
		$\delta\ ^{13}C$ ~ Sex	female	-25.662	20	1.000
			male	-25.705		
		$\delta\ ^{15}N$ ~ Habitat	agricultural	6.9245	32	0.093
			urban	4.534		
		$\delta\ ^{13}C$ ~ Habitat	agricultural	-25.693	18	0.833
			urban	-25.686		
H. rufipes	**Cuticula**	$\delta\ ^{15}N$ ~ Sex	female	6.287	55	0.739
			male	5.495		
		$\delta\ ^{13}C$ ~ Sex	female	-25.755	61	0.436
			male	-27.053		
		$\delta\ ^{15}N$ ~ Habitat	agricultural	6.540	80	**0.023**
			urban	4.273		
		$\delta\ ^{13}C$ ~ Habitat	agricultural	-25.755	62	0.393
			urban	-27.019		
	Legs	$\delta\ ^{15}N$ ~ Sex	female	6.307	44	0.684
			male	6.344		
		$\delta\ ^{13}C$ ~ Sex	female	-24.870	64	0.315
			male	-27.161		
		$\delta\ ^{15}N$ ~ Habitat	agricultural	6.718	77	**0.043**
			urban	5.304		
		$\delta\ ^{13}C$ ~ Habitat	agricultural	-24.870	64	0.315
			urban	-27.144		
	Muscles	$\delta\ ^{15}N$ ~ Sex	female	7.363	51	0.971
			male	6.749		
		$\delta\ ^{13}C$ ~ Sex	female	-25.088	59	0.529
			male	-26.320		
		$\delta\ ^{15}N$ ~ Habitat	agricultural	7.557	85	**0.007**
			urban	5.053		
		$\delta\ ^{13}C$ ~ Habitat	agricultural	-25.088	68	0.190
			urban	-26.491		

Table A4 Stable ^{14}N and ^{13}C isotope enrichments between cuticula, legs, and muscles of *Harpalus affinis* and *H. rufipes* from agricultural and urban habitats. Results of Kruskal-Wallis rank sum tests for comparisons between tissues of beetles originated from agricultural and urban habitats.

Species	Habitat	Comparison	Tissue	Medians	Chi-squared	df	p-value
H. affinis	**Agicultural**	δ 13C ~ Tissue	Cuticula	-26.3885	2.2999	2	0.317
			Legs	-26.3005			
			Muscles	-25.6925			
		δ 15N ~ Tissue	Cuticula	6.2830	1.2739	2	0.529
			Legs	6.3840			
			Muscles	6.9245			
	Urban	δ 13C ~ Tissue	Cuticula	-26.3105	1.5102	2	0.470
			Legs	-26.3130			
			Muscles	-25.6860			
		δ 15N ~ Tissue	Cuticula	2.8390	3.3729	2	0.185
			Legs	2.9185			
			Muscles	4.5340			
H. rufipse	**Agricultural**	δ 13C ~ Tissue	Cuticula	-25.7545	0.34323	2	0.8423
			Legs	-24.8695			
			Muscles	-25.0880			
		δ 15N ~ Tissue	Cuticula	6.5395	2.6039	2	0.272
			Legs	6.7180			
			Muscles	7.5579			
	Urban	δ 13C ~ Tissue	Cuticula	-27.019	0.63304	2	0.7287
			Legs	-27.144			
			Muscles	-26.491			
		δ 15N ~ Tissue	Cuticula	4.2730	0.018065	2	0.991
			Legs	5.3040			
			Muscles	5.0525			

Table A5 Stable ^{15}N and ^{13}C isotope enrichments (in ‰) in cuticula, legs, and muscles of *Harpalus affinis* and *H. rufipes* from agricultural and urban habitats. Results of Levene´s Test for Homogeneity of Variance, centre = median. Significant p-values are given in bold.

Species	Tissue	Comparison	Medians		Df	F-value	p-value
H. affinis	Cuticula	$\delta\ ^{15}N$ ~ Habitat	agricultural	9.944	18	0.0362	0.851
			urban	7.225			
		$\delta\ ^{13}C$ ~ Habitat	agricultural	1.240	18	0.049	0.827
			urban	2.114			
	Legs	$\delta\ ^{15}N$ ~ Habitat	agricultural	10.163	18	0.0221	0.884
			urban	4.720			
		$\delta\ ^{13}C$ ~ Habitat	agricultural	3.017	18	0.0457	0.833
			urban	3.528			
	Muscles	$\delta\ ^{15}N$ ~ Habitat	agricultural	9.262	18	0.5384	0.478
			urban	3.472			
		$\delta\ ^{13}C$ ~ Habitat	agricultural	0.835	18	0.6774	0.428
			urban	3.078			
H. rufipes	Cuticula	$\delta\ ^{15}N$ ~ Habitat	agricultural	1.877	18	1.7107	0.207
			urban	3.894			
		$\delta\ ^{13}C$ ~ Habitat	agricultural	13.396	18	0.0137	0.908
			urban	19.419			
	Legs	$\delta\ ^{15}N$ ~ Habitat	agricultural	1.255	18	4.0902	0.0583
			urban	4.932			
		$\delta\ ^{13}C$ ~ Habitat	agricultural	18.588	18	0.3294	0.573
			urban	24.233			
	Muscles	$\delta\ ^{15}N$ ~ Habitat	agricultural	0.778	18	7.9687	**0.011***
			urban	4.713			
		$\delta\ ^{13}C$ ~ Habitat	agricultural	8.678	18	0.1067	0.748
			urban	16.596			

Table B Sample areas within Berlin or Brandenburg of *Harpalus affinis* specimens with Region (urban; rural), district, Further sampling site information, Habitat if available (urban; agricultural landscape), sex (f = female; m = male), GPS coordinates (latitude; longitude), sampling year, time period, measurements of standardized body size in mm (SBL), and repeated SBL measurements in mm of a subset of specimens.

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
1	Berlin	urban	Mitte	Mitte	urban	f	52529000	13359604	1901	1892-1949	8,88	-
2	Berlin	urban	Spandau	Spandau	-	f	52.540.834	13.189.543	1901	1892-1949	9,06	-
3	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	f	52428895	13308185	1904	1892-1949	9,86	-
4	Berlin	urban	Charlottenburg-Wilmersdorf	Wilmersdorf	-	f	52491663	13314148	1905	1892-1949	9,50	-
5	Berlin	urban	Charlottenburg-Wilmersdorf	Wilmersdorf	-	f	52491663	13314148	1905	1892-1949	9,63	-
6	Berlin	urban	Steglitz-Zehlendorf	Steglitz	-	f	52456127	13335341	1906	1892-1949	9,22	-
7	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	9,45	-
8	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	8,95	-
9	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	9,37	-
10	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	8,14	-
11	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	8,45	-
12	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	9,32	-
13	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	9,60	-
14	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1906	1892-1949	9,50	-
15	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	f	52428895	13308185	1908	1892-1949	8,94	-
16	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	f	52428895	13308185	1908	1892-1949	9,69	-
17	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	f	52428895	13308185	1908	1892-1949	8,88	-
18	Berlin	urban	Tempelhof-Schoeneberg	Lichtenrade	-	f	52395878	13402458	1909	1892-1949	8,26	-
19	Berlin	urban	Tempelhof-Schoeneberg	Lichtenrade	-	f	52395878	13402458	1909	1892-1949	9,02	-
20	Berlin	urban	Treptow-Koepenick	Gruenau	-	f	52.409.002	13.587.712	1909	1892-1949	9,01	-
21	Berlin	urban	Spandau	Spandau	-	f	52.540.834	13.189.543	1911	1892-1949	8,48	-
22	Berlin	urban	Steglitz-Zehlendorf	Zehlendorf	-	f	52437752	13253738	1913	1892-1949	9,38	-
23	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	f	52428895	13308185	1915	1892-1949	9,04	-
24	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	f	52428895	13308185	1915	1892-1949	9,13	-
25	Berlin	urban	Pankow	Buch	-	f	52642189	13486930	1919	1892-1949	9,12	-
26	Berlin	urban	Pankow	Weissensee	-	f	52.551.752	13.461.638	1927	1892-1949	9,63	9,69

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
27	Berlin	urban	Spandau	Spandau	-	f	52.540.834	13.189.543	1934	1892-1949	10,06	-
28	Berlin	urban	Mitte	Wedding, Ploetzensee	-	f	52544026	13331312	1935	1892-1949	7,64	-
29	Berlin	urban	Marzahn-Hellersdorf	Kaulsdorf	-	f	52.509.750	13.588.086	1943	1892-1949	8,08	-
30	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1947	1892-1949	8,63	-
31	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1947	1892-1949	8,20	-
32	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1947	1892-1949	9,69	-
33	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1967	1957-1998	8,51	-
34	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1967	1957-1998	8,88	-
35	Berlin	urban	Marzahn-Hellersdorf	Hellersdorf	-	f	52.538.769	13.599.204	1968	1957-1998	9,50	-
36	Berlin	urban	Marzahn-Hellersdorf	Hellersdorf	-	f	52.538.769	13.599.204	1968	1957-1998	9,50	-
37	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1968	1957-1998	9,16	-
38	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1968	1957-1998	9,31	-
39	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1968	1957-1998	8,82	-
40	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1968	1957-1998	9,07	-
41	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1968	1957-1998	8,51	-
42	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1968	1957-1998	8,83	-
43	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1969	1957-1998	5,30	-
44	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1969	1957-1998	8,88	-
45	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1969	1957-1998	9,50	-
46	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1969	1957-1998	8,51	-
47	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1969	1957-1998	7,71	-
48	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1969	1957-1998	8,76	-
49	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1969	1957-1998	8,07	-
50	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1970	1957-1998	8,82	-
51	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1970	1957-1998	9,44	-
52	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1970	1957-1998	9,57	-
53	Berlin	urban	Lichtenberg	Friedrichsfelde, Tierpark	-	f	52502028	13529810	1971	1957-1998	8,82	-
54	Berlin	urban	Pankow	Weissensee	-	f	52.551.752	13.461.638	1971	1957-1998	9,50	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
55	Berlin	urban	Pankow	Weissensee	-	f	52.551.752	13.461.638	1971	1957-1998	8,76	-
56	Berlin	urban	Pankow	Weissensee	-	f	52.551.752	13.461.638	1971	1957-1998	8,07	-
57	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1972	1957-1998	8,88	-
58	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1972	1957-1998	8,94	-
59	Berlin	urban	Tempelhof-Schoeneberg	Marienfelde	-	f	52403966	13367800	1973	1957-1998	9,39	-
60	Berlin	urban	Tempelhof-Schoeneberg	Marienfelde	-	f	52403966	13367800	1973	1957-1998	9,32	-
61	Berlin	urban	Tempelhof-Schoeneberg	Marienfelde	-	f	52403966	13367800	1973	1957-1998	9,45	-
62	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1975	1957-1998	9,63	-
63	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1975	1957-1998	8,63	-
64	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1975	1957-1998	8,14	-
65	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1975	1957-1998	9,38	-
66	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1975	1957-1998	9,50	-
67	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1975	1957-1998	9,25	-
68	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.985	13.428.349	1975	1957-1998	8,39	-
69	Berlin	urban	Lichtenberg	Lichtenberg	-	f	52.542.437	13.486.904	1976	1957-1998	8,88	-
70	Berlin	urban	Lichtenberg	Rummelsburg	-	f	52.498.296	13.486.759	1976	1957-1998	9,19	-
71	Berlin	urban	Lichtenberg	Malchow	-	f	52578259	13488295	1977	1957-1998	8,63	8,67
72	Berlin	urban	Lichtenberg	Lichtenberg	-	f	52.542.437	13.486.904	1977	1957-1998	8,39	-
73	Berlin	urban	Pankow	Heinersdorf	-	f	52.568.107	13.436.845	1977	1957-1998	9,50	-
74	Berlin	urban	Pankow	Heinersdorf	-	f	52.568.107	13.436.845	1977	1957-1998	9,19	-
75	Berlin	urban	Pankow	Heinersdorf	-	f	52.568.107	13.436.845	1977	1957-1998	9,32	-
76	Berlin	urban	Treptow-Koepenick	Friedrichshagen	-	f	52.460.103	13.630.991	1978	1957-1998	9,25	-
77	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.574	13.558.199	1979	1957-1998	8,97	-
78	Berlin	urban	Lichtenberg	Malchow	-	f	52578259	13488295	1980	1957-1998	9,30	-
79	Berlin	urban	Tempelhof-Schoeneberg	Marienfelde	-	f	52404385	13362822	1980	1957-1998	8,51	-
80	Berlin	urban	Tempelhof-Schoeneberg	Marienfelde	-	f	52404385	13362822	1980	1957-1998	9,81	-
81	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	f	52.550.087	13.560.002	1986	1957-1998	8,76	-
82	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	f	52.550.087	13.560.002	1986	1957-1998	9,07	-
83	Berlin	urban	Lichtenberg	Hohenschoenhausen	-	f	52566173	13520207	1987	1957-1998	8,63	-

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84	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	f	52.550.087	13.560.002	1987	1957-1998	8,82	-
85	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	f	52.550.087	13.560.002	1987	1957-1998	9,50	-
86	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	f	52.550.087	13.560.002	1987	1957-1998	9,07	-
87	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	f	52.550.087	13.560.002	1987	1957-1998	9,44	-
88	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	f	52.550.087	13.560.002	1987	1957-1998	8,75	-
89	Berlin	urban	Reinickendorf	Wittenau	-	f	52.589.187	13.329.318	1988	1957-1998	9,32	-
90	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1992	1957-1998	8,39	-
91	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1992	1957-1998	8,32	-
92	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1992	1957-1998	8,76	-
93	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1992	1957-1998	8,45	-
94	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	f	52.506.685	13.615.582	1992	1957-1998	9,01	-
95	Berlin	urban	Friedrichshain-Kreuzberg	Neukoelln	-	f	52.439.269	13.444.629	1993	1957-1998	9,88	-
96	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	9,63	-
97	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	9,38	-
98	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	9,27	-
99	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	8,88	-
100	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	9,32	-
101	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	9,01	-
102	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	8,82	-
103	Berlin	urban	Treptow-Koepenick	Johannistal	-	f	52.441.568	13.509.696	1993	1957-1998	9,01	-
104	Berlin	urban	Treptow-Koepenick	Altglienicke	-	f	52.409.770	13.552.385	1993	1957-1998	8,20	-
105	Berlin	urban	Treptow-Koepenick	Treptow	-	f	52.450.000	13.566.667	1993	1957-1998	8,76	-
106	Berlin	urban	Friedrichshain-Kreuzberg	Neukoelln	-	f	52.439.269	13.444.629	1994	1957-1998	9,01	-
107	Berlin	urban	Treptow-Koepenick	Treptow	-	f	52.450.000	13.566.667	1994	1957-1998	9,69	-
108	Berlin	urban	Charlottenburg-Wilmersdorf	Grunewald, Am Postfenn	urban	f	52.500.580	13.224.440	2017	2016-2017	8,45	-
109	Berlin	urban	Mitte	Tiergarten	urban	f	52.514.260	13.375.760	2017	2016-2017	8,45	-
110	Berlin	urban	Mitte	Tiergarten	urban	f	52.514.260	13.375.760	2017	2016-2017	8,88	-
111	Berlin	urban	Neukoelln	Fritz-Erler-Allee	urban	f	52.436.530	13.451.440	2017	2016-2017	8,20	-
112	Berlin	urban	Pankow	Karow	urban	f	52.616.620	13.448.110	2017	2016-2017	8,88	-

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113	Berlin	urban	Spandau	Gatow	urban	f	52.477.370	13.129.650	2017	2016-2017	9,07	-
114	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	f	52.475.410	13.406.030	2017	2016-2017	8,76	-
115	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	f	52.475.410	13.406.030	2017	2016-2017	9,25	-
116	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	f	52.475.410	13.406.030	2017	2016-2017	8,63	-
117	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	f	52.475.410	13.406.030	2017	2016-2017	9,57	-
118	Berlin	urban	Treptow-Koepenick	AS Stubenrauchstrasse	urban	f	52.434.290	13.499.020	2017	2016-2017	9,50	-
119	Berlin	urban	Mitte	City centre	urban	m	52.530.644	13.383.068	1901	1892-1949	8,20	-
120	Berlin	urban	Mitte	City centre	urban	m	52.530.644	13.383.068	1901	1892-1949	9,32	-
121	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1902	1892-1949	8,45	-
122	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1902	1892-1949	8,57	-
123	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	m	52.430.884	13.192.662	1904	1892-1949	7,89	-
124	Berlin	urban	Charlottenburg-Wilmersdorf	Wilmersdorf	-	m	52.500.000	13.283.333	1905	1892-1949	8,57	-
125	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,63	-
126	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,39	-
127	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,73	-
128	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	9,32	-
129	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,94	-
130	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,48	-
131	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,82	-
132	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,20	-
133	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,42	-
134	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	9,11	-
135	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,61	-
136	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,07	-
137	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,88	-
138	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	10,30	-
139	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,60	-
140	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,57	-
141	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	8,76	-

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142	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	9,01	-
143	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1906	1892-1949	9,07	-
144	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1907	1892-1949	8,20	-
145	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1908	1892-1949	8,14	-
146	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	m	52.430.884	13.192.662	1908	1892-1949	8,94	-
147	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1909	1892-1949	8,76	-
148	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1909	1892-1949	8,20	-
149	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1909	1892-1949	8,32	-
150	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1909	1892-1949	8,45	-
151	Berlin	urban	Treptow-Koepenick	Gruenau	-	m	52.409.002	13.587.712	1909	1892-1949	8,33	-
152	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1909	1892-1949	9,07	-
153	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1913	1892-1949	8,70	-
154	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	m	52.430.884	13.192.662	1915	1892-1949	8,86	-
155	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	m	52.430.884	13.192.662	1915	1892-1949	7,83	-
156	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1918	1892-1949	8,70	-
157	Berlin	urban	Marzahn-Hellersdorf	Kaulsdorf	-	m	52.509.750	13.588.086	1922	1892-1949	9,07	-
158	Berlin	urban	Treptow-Koepenick	Wuhlheide	-	m	52.462.275	13.534.695	1935	1892-1949	8,65	-
159	Berlin	urban	Treptow-Koepenick	Wuhlheide	-	m	52.462.275	13.534.695	1936	1892-1949	8,39	8,45
160	Berlin	urban	Spandau	Staaken	-	m	52.533.834	13.140.730	1937	1892-1949	8,93	-
161	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1943	1892-1949	9,19	-
162	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1944	1892-1949	8,14	-
163	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1944	1892-1949	9,12	9,25
164	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1946	1892-1949	8,76	-
165	Berlin	urban	Friedrichshain-Kreuzberg	Friedrichshain	-	m	52.511.667	13.447.702	1947	1892-1949	8,26	-
166	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1947	1892-1949	8,57	-
167	Berlin	urban	Tempelhof-Schoeneberg	Tempelhof	-	m	52.472.247	13.388.525	1957	1957-1998	8,57	8,63
168	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1966	1957-1998	8,07	-
169	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1967	1957-1998	9,01	-
170	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1967	1957-1998	8,51	-

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171	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1967	1957-1998	13,11	-
172	Berlin	urban	Marzahn-Hellersdorf	Kaulsdorf	-	m	52.509.750	13.588.086	1968	1957-1998	8,88	-
173	Berlin	urban	Marzahn-Hellersdorf	Hellersdorf	-	m	52.538.769	13.599.204	1968	1957-1998	8,51	8,57
174	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1968	1957-1998	8,94	-
175	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1968	1957-1998	9,20	-
176	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1968	1957-1998	8,82	-
177	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1968	1957-1998	9,25	-
178	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1968	1957-1998	8,82	-
179	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	8,76	-
180	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	8,32	-
181	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	8,82	-
182	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	7,95	-
183	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	8,63	-
184	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	8,50	8,51
185	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	7,70	-
186	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1969	1957-1998	8,63	-
187	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1969	1957-1998	9,50	-
188	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1969	1957-1998	8,57	-
189	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1969	1957-1998	8,33	-
190	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1969	1957-1998	9,13	-
191	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1969	1957-1998	8,62	-
192	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1969	1957-1998	9,69	-
193	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1970	1957-1998	7,58	-
194	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1971	1957-1998	9,75	-
195	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1971	1957-1998	7,95	-
196	Berlin	urban	Pankow	Weissensee	-	m	52.551.752	13.461.638	1971	1957-1998	8,51	-
197	Berlin	urban	Tempelhof-Schoeneberg	Marienfelde	-	m	52.414.019	13.368.658	1971	1957-1998	9,13	-
198	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1972	1957-1998	8,25	-
199	Berlin	urban	Marzahn-Hellersdorf	Kaulsdorf	-	m	52.509.750	13.588.086	1972	1957-1998	8,70	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
200	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1972	1957-1998	8,82	-
201	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1972	1957-1998	8,20	-
202	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1972	1957-1998	8,57	-
203	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1972	1957-1998	8,70	-
204	Berlin	urban	Treptow-Koepenik	Koepenik	-	m	52.437.267	13.604.787	1972	1957-1998	8,32	-
205	Berlin	urban	Tempelhof-Schoeneberg	Marienfelde	-	m	52.414.019	13.368.658	1973	1957-1998	9,25	-
206	Berlin	urban	Lichtenberg	Lichtenberg	-	m	52.542.437	13.486.904	1975	1957-1998	8,88	-
207	Berlin	urban	Lichtenberg	Lichtenberg	-	m	52.542.437	13.486.904	1975	1957-1998	7,39	-
208	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1975	1957-1998	8,40	-
209	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1975	1957-1998	8,63	-
210	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.574	13.558.199	1975	1957-1998	8,39	-
211	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1975	1957-1998	7,83	-
212	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1975	1957-1998	8,20	8,26
213	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1975	1957-1998	8,50	-
214	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1975	1957-1998	8,20	-
215	Berlin	urban	Lichtenberg	Lichtenberg	-	m	52.542.437	13.486.904	1976	1957-1998	8,57	-
216	Berlin	urban	Lichtenberg	Rummelsburg	-	m	52.498.296	13.486.759	1976	1957-1998	9,07	-
217	Berlin	urban	Pankow	Heinersdorf	-	m	52.568.107	13.436.845	1977	1957-1998	8,33	-
218	Berlin	urban	Pankow	Heinersdorf	-	m	52.568.107	13.436.845	1977	1957-1998	8,27	-
219	Berlin	urban	Pankow	Heinersdorf	-	m	52.568.107	13.436.845	1977	1957-1998	7,89	-
220	Berlin	urban	Pankow	Niederschoenhausen	-	m	52.576.153	13.390.058	1977	1957-1998	8,70	-
221	Berlin	urban	Treptow-Koepenick	Friedrichshagen	-	m	52.460.103	13.630.991	1978	1957-1998	8,94	-
222	Berlin	urban	Pankow	Heinersdorf	-	m	52.568.107	13.436.845	1979	1957-1998	7,95	-
223	Berlin	urban	Pankow	Heinersdorf	-	m	52.568.107	13.436.845	1979	1957-1998	8,83	-
224	Berlin	urban	Pankow	Heinersdorf	-	m	52.568.107	13.436.845	1979	1957-1998	8,88	-
225	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1979	1957-1998	9,14	-
226	Berlin	urban	Lichtenberg	Lichtenberg	-	m	52.542.437	13.486.904	1980	1957-1998	7,83	-
227	Berlin	urban	Lichtenberg	Lichtenberg	-	m	52.542.437	13.486.904	1980	1957-1998	8,39	-
228	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.985	13.428.349	1980	1957-1998	8,94	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
229	Berlin	urban	Pankow	Pankow	-	m	52.597.603	13.420.919	1981	1957-1998	7,58	-
230	Berlin	urban	Reinickendorf	Luebars	-	m	52.618.293	13.357.601	1981	1957-1998	8,60	-
231	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1981	1957-1998	8,45	-
232	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1984	1957-1998	8,57	-
233	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1986	1957-1998	9,19	-
234	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1986	1957-1998	8,01	-
235	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1986	1957-1998	8,45	-
236	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1986	1957-1998	8,50	-
237	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1986	1957-1998	8,07	-
238	Berlin	urban	Friedrichshain-Kreuzberg	Landsberger Allee	urban	m	52.535.577	13.521.718	1987	1957-1998	9,01	-
239	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1987	1957-1998	8,88	-
240	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1987	1957-1998	7,27	-
241	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1987	1957-1998	8,70	-
242	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1987	1957-1998	8,70	-
243	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1987	1957-1998	9,25	-
244	Berlin	urban	Marzahn-Hellersdorf	Marzahn	-	m	52.550.087	13.560.002	1987	1957-1998	9,13	-
245	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1988	1957-1998	8,39	-
246	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1988	1957-1998	8,82	-
247	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1988	1957-1998	8,88	-
248	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1988	1957-1998	8,45	-
249	Berlin	urban	Reinickendorf	Wittenau	-	m	52.589.187	13.329.318	1988	1957-1998	8,82	-
250	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,82	-
251	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,88	-
252	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,81	-
253	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,20	-
254	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,70	-
255	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,45	-
256	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,51	-
257	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,51	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
258	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	8,45	-
259	Berlin	urban	Marzahn-Hellersdorf	Mahlsdorf	-	m	52.506.685	13.615.582	1992	1957-1998	9,07	-
260	Berlin	urban	Friedrichshain-Kreuzberg	Neukoelln	-	m	52.439.269	13.444.629	1993	1957-1998	9,50	-
261	Berlin	urban	Spandau	Spandau	-	m	52.540.834	13.189.543	1993	1957-1998	8,94	-
262	Berlin	urban	Spandau	Spandau	-	m	52.540.834	13.189.543	1993	1957-1998	8,88	-
263	Berlin	urban	Spandau	Spandau	-	m	52.540.834	13.189.543	1993	1957-1998	8,45	-
264	Berlin	urban	Spandau	Spandau	-	m	52.540.834	13.189.543	1993	1957-1998	8,71	-
265	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	9,52	-
266	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	8,56	-
267	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	8,57	-
268	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	8,94	-
269	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	8,88	-
270	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	9,33	-
271	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	8,14	-
272	Berlin	urban	Treptow-Koepenick	Johannistal	-	m	52.441.568	13.509.696	1993	1957-1998	8,14	-
273	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1993	1957-1998	9,07	-
274	Berlin	urban	Treptow-Koepenick	Altglienicke	-	m	52.409.770	13.552.385	1993	1957-1998	7,64	-
275	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1993	1957-1998	9,01	-
276	Berlin	urban	Pankow	Blankenburg	-	m	52.591.683	13.455.444	1994	1957-1998	8,70	-
277	Berlin	urban	Treptow-Koepenick	Johannistal	-	m	52.441.568	13.509.696	1994	1957-1998	8,88	-
278	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1994	1957-1998	9,30	-
279	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1994	1957-1998	8,76	-
280	Berlin	urban	Treptow-Koepenick	Treptow	-	m	52.450.000	13.566.667	1998	1957-1998	8,51	-
281	Berlin	urban	Charlottenburg-Wilmersdorf	Grunewald, Am Postfenn	urban	m	52,500,580	13,224,440	2017	2016-2017	8,14	-
282	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,510	13,373,530	2017	2016-2017	11,68	-
283	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,260	13,375,760	2017	2016-2017	8,57	-
284	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,260	13,375,760	2017	2016-2017	8,39	-
285	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,510	13,373,530	2017	2016-2017	8,45	-
286	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,260	13,375,760	2017	2016-2017	5,78	-

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287	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,260	13,375,760	2017	2016-2017	8,20	-
288	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,260	13,375,760	2017	2016-2017	8,39	-
289	Berlin	urban	Pankow	Buch	urban	m	52,630,440	13,484,280	2017	2016-2017	11,24	-
290	Berlin	urban	Pankow	Karow	urban	m	52,616,620	13,448,110	2017	2016-2017	8,70	-
291	Berlin	urban	Pankow	Karow	urban	m	52,616,620	13,448,110	2017	2016-2017	9,07	-
292	Berlin	urban	Pankow	Karow	urban	m	52,616,620	13,448,110	2017	2016-2017	9,07	-
293	Berlin	urban	Pankow	Buch	urban	m	52,630,440	13,484,280	2017	2016-2017	8,39	-
294	Berlin	urban	Spandau	Spandauer Forst, Eiskeller	urban	m	52,583,310	13,145,720	2017	2016-2017	8,70	-
295	Berlin	urban	Spandau	Gatow	urban	m	52,477,370	13,129,650	2017	2016-2017	8,63	-
296	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	m	52,475,410	13,406,030	2017	2016-2017	9,44	-
297	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	m	52,475,410	13,406,030	2017	2016-2017	9,19	-
298	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	m	52,475,410	13,406,030	2017	2016-2017	9,38	-
299	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	m	52,475,410	13,406,030	2017	2016-2017	9,13	-
300	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	urban	m	52,475,410	13,406,030	2017	2016-2017	8,88	-
301	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	f	52555437	13882815	1893	1892-1949	9,13	-
302	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	f	52474314	13820982	1899	1892-1949	8,45	-
303	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	f	52474314	13820982	1899	1892-1949	8,02	-
304	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	f	52557800	13036158	1909	1892-1949	7,80	-
305	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	f	52557800	13036158	1909	1892-1949	8,57	-
306	Brandenburg	rural	Havelland	Nauen	-	f	52610488	12832286	1910	1892-1949	8,26	-
307	Brandenburg	rural	Havelland	Dallgow-Doeberitz	-	f	52518350	13069026	1923	1892-1949	8,83	-
308	Brandenburg	rural	Havelland	Dallgow-Doeberitz	-	f	52518350	13069026	1924	1892-1949	8,06	-
309	Brandenburg	rural	Havelland	Nauen	-	f	52610488	12832286	1927	1892-1949	9,24	-
310	Brandenburg	rural	Havelland	Brieselang	-	f	52591192	12974592	1927	1892-1949	8,51	-
311	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	f	52121623	13404372	1930	1892-1949	8,88	-
312	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	f	52121623	13404372	1930	1892-1949	9,25	-
313	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	f	52121623	13404372	1930	1892-1949	8,39	-
314	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	f	52121623	13404372	1930	1892-1949	9,80	-
315	Brandenburg	rural	Maerkisch-Oderland	Herzfelde in Ruedersdorf	-	f	52482295	13861546	1931	1892-1949	9,81	-

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316	Brandenburg	rural	Barnim	Tiefensee	-	f	52667373	13821467	1932	1892-1949	8,39	-
317	Brandenburg	rural	Barnim	Groß Schoenebeck	-	f	52919234	13573580	1932	1892-1949	9,25	-
318	Brandenburg	rural	Teltow-Flaeming	Großmachnower Weinberg	-	f	52266582	13503082	1932	1892-1949	9,75	-
319	Brandenburg	rural	Elbe-Elster	Schoenborn (Eichwalde)	-	f	51582453	13486844	1933	1892-1949	9,94	-
320	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	f	52121623	13404372	1937	1892-1949	8,94	-
321	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	f	52121623	13404372	1937	1892-1949	8,57	-
322	Brandenburg	rural	Teltow-Flaeming	Brieselang	-	f	52591192	12974592	1941	1892-1949	8,82	-
323	Brandenburg	rural	Dahme-Spreewald	Wildau	-	f	52313717	13628312	1942	1892-1949	8,94	-
324	Brandenburg	rural	Havelland	Nauen	-	f	52610488	12832286	1942	1892-1949	9,81	9,72
325	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	f	52258812	13319982	1942	1892-1949	8,76	-
326	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	f	52258812	13319982	1942	1892-1949	9,73	-
327	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	f	52258812	13319982	1942	1892-1949	8,39	-
328	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	f	52258812	13319982	1942	1892-1949	9,34	-
329	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	f	52258812	13319982	1942	1892-1949	9,44	-
330	Brandenburg	rural	Dahme-Spreewald	Wildau	-	f	52313717	13628312	1943	1892-1949	9,26	-
331	Brandenburg	rural	Dahme-Spreewald	Wildau	-	f	52313717	13628312	1943	1892-1949	8,57	-
332	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	f	52557800	13036158	1943	1892-1949	8,63	-
333	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	f	52557800	13036158	1943	1892-1949	8,77	8,67
334	Brandenburg	rural	Maerkisch-Oderland	Herzfelde in Ruedersdorf	-	f	52482295	13861546	1943	1892-1949	8,88	-
335	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	f	52459673	13836088	1943	1892-1949	10,01	-
336	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	-	f	52 316740	13 410668	1947	1892-1949	8,70	-
337	Brandenburg	rural	Barnim	Chorin	-	f	52896295	13905457	1949	1892-1949	10,30	-
338	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	f	52677445	13373545	1949	1892-1949	8,88	-
339	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	f	52677445	13373545	1949	1892-1949	11,86	-
340	Brandenburg	rural	Maerkisch-Oderland	Strausberg-Torfhaus	-	f	52517437	13842452	1965	1957-1998	9,19	-
341	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	f	52652879	13334172	1967	1957-1998	9,63	-
342	Brandenburg	rural	Barnim	Wandlitz Lotschesee	-	f	52811314	13501236	1968	1957-1998	9,07	-
343	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	f	52459673	13836088	1969	1957-1998	9,44	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
344	Brandenburg	rural	Barnim	Ahrensfelde	-	f	52594215	13575544	1970	1957-1998	8,82	-
345	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	f	52604129	13628552	1970	1957-1998	9,57	-
346	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	f	52604129	13628552	1970	1957-1998	9,13	-
347	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	f	52604129	13628552	1970	1957-1998	8,26	-
348	Brandenburg	rural	Dahme-Spreewald	Egsdorf Teupitzer See	-	f	52127990	13597811	1970	1957-1998	8,63	-
349	Brandenburg	rural	Oder-Spree	Gruenheide bei Erkner	-	f	52426158	13864626	1970	1957-1998	9,63	9,57
350	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel	-	f	52339170	12467982	1970	1957-1998	8,57	-
351	Brandenburg	rural	Barnim	Basdorf in Wandlitz	-	f	52701195	13425686	1971	1957-1998	7,76	-
352	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	f	52701496	13475292	1972	1957-1998	8,94	-
353	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	f	52701496	13475292	1972	1957-1998	9,25	-
354	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	f	52701496	13475292	1972	1957-1998	8,82	-
355	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	f	52701496	13475292	1972	1957-1998	9,07	-
356	Brandenburg	rural	Oberhavel	Schildow-Moenchmuehle	-	f	52649469	13390917	1972	1957-1998	9,57	-
357	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	f	52701496	13475292	1973	1957-1998	8,82	-
358	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	f	52677445	13373545	1973	1957-1998	9,17	-
359	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	f	52677445	13373545	1973	1957-1998	8,76	-
360	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	f	52652879	13334172	1973	1957-1998	9,07	-
361	Brandenburg	rural	Oberhavel	Hohen Neuendorf Kreis Oranienburg	-	f	52647518	13263836	1973	1957-1998	8,76	-
362	Brandenburg	rural	Dahme-Spreewald	Wernsdorf Kreis Koenigs Wusterhausen	-	f	52347094	13699639	1974	1957-1998	7,14	-
363	Brandenburg	rural	Dahme-Spreewald	Wernsdorf Kreis Koenigs Wusterhausen	-	f	52347094	13699639	1974	1957-1998	9,13	-
364	Brandenburg	rural	Oberhavel	Schildow	-	f	52644126	13361704	1974	1957-1998	9,50	-
365	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	f	52604129	13628552	1975	1957-1998	9,66	-
366	Brandenburg	rural	Dahme-Spreewald	Kablow Kreis Koenigs Wusterhausen	-	f	52299745	13738424	1975	1957-1998	8,82	-
367	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,19	-
368	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,01	-
369	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,40	-
370	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,88	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
371	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,66	-
372	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,63	-
373	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,62	-
374	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1975	1957-1998	9,13	-
375	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	f	52416667	14532821	1975	1957-1998	9,13	-
376	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	f	52416667	14532821	1975	1957-1998	8,88	-
377	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	f	52416667	14532821	1975	1957-1998	9,76	-
378	Brandenburg	rural	Oberhavel	Henningsdorf Kreis Oranienburg	-	f	52618226	13185346	1975	1957-1998	10,31	-
379	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	f	52652879	13334172	1977	1957-1998	8,70	-
380	Brandenburg	rural	Potsdam-Mittelmark	Holz-Berg in Rietz, Rietzer See, natural reserve	-	f	52366718	12630587	1977	1957-1998	9,64	-
381	Brandenburg	rural	Oder-Spree	Fuerstenwalde, Wernsdorfer See, protected landscape	-	f	52384693	13712268	1978	1957-1998	9,50	-
382	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	f	52485625	12906010	1978	1957-1998	9,19	-
383	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel	-	f	52339170	12467982	1978	1957-1998	8,39	-
384	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	f	52465122	14479306	1979	1957-1998	9,07	9,07
385	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	f	52485625	12906010	1979	1957-1998	8,20	-
386	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	f	52485625	12906010	1979	1957-1998	7,95	-
387	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	f	52485625	12906010	1979	1957-1998	8,20	-
388	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	f	52485625	12906010	1979	1957-1998	8,76	-
389	Brandenburg	rural	Potsdam-Mittelmark	Island Buhnenwerder in Plauer See bei Kirchmoeser, protected landscape	-	f	52394386	12471018	1979	1957-1998	8,78	-
390	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel	-	f	52339170	12467982	1979	1957-1998	8,45	-
391	Brandenburg	rural	Maerkisch-Oderland	Muencheberg	-	f	52515053	14075518	1980	1957-1998	7,70	-
392	Brandenburg	rural	Maerkisch-Oderland	Muencheberg	-	f	52515053	14075518	1980	1957-1998	9,18	-
393	Brandenburg	rural	Oberhavel	Klein-Mutz Kreis Zehdenik	-	f	52949970	13290679	1980	1957-1998	8,70	-
394	Brandenburg	rural	Oder-Spree	Gruenheide (surroundings)	-	f	52428670	13887972	1980	1957-1998	8,57	-
395	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	f	52630479	13356897	1981	1957-1998	8,88	-
396	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	f	52652879	13334172	1981	1957-1998	8,76	-

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397	Brandenburg	rural	Oberhavel	Neuendorf in Loewenberger Land	-	f	52836414	13119294	1982	1957-1998	8,39	-
398	Brandenburg	rural	Teltow-Flaeming	Großbeeren	-	f	52357527	13316374	1982	1957-1998	9,25	-
399	Brandenburg	rural	Teltow-Flaeming	Großbeeren	-	f	52357527	13316374	1982	1957-1998	9,50	9,38
400	Brandenburg	rural	Barnim	Barnim	-	f	52993806	13432426	1983	1957-1998	8,45	-
401	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	f	52557107	13885561	1983	1957-1998	9,48	9,49
402	Brandenburg	rural	Oder-Spree	Erkner	-	f	52395934	13763690	1983	1957-1998	9,19	-
403	Brandenburg	rural	Oder-Spree	Erkner	-	f	52395934	13763690	1983	1957-1998	9,81	-
404	Brandenburg	rural	Oder-Spree	Erkner	-	f	52395934	13763690	1983	1957-1998	9,39	9,32
405	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	f	52652879	13334172	1985	1957-1998	8,88	-
406	Brandenburg	rural	Oderspreewald-Lausitz	Großkoschen in Senftenberg	-	f	51489227	14060600	1985	1957-1998	9,50	-
407	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	f	52416667	14532821	1986	1957-1998	10,00	-
408	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	f	52557107	13885561	1987	1957-1998	9,19	-
409	Brandenburg	rural	Spree-Neiße	Cottbus, inland dunes	-	f	51779871	14428495	1987	1957-1998	9,63	9,69
410	Brandenburg	rural	Potsdam-Mittelmark	Toepchin Werder	-	f	52390937	12877433	1991	1957-1998	8,82	-
411	Brandenburg	rural	Teltow-Flaeming	Hostfelde in Zossen	-	f	52216640	13407134	1991	1957-1998	8,51	-
412	Brandenburg	rural	Oberhavel	Mildenberg in Zehdenick	-	f	53027335	13302829	1998	1957-1998	8,80	-
413	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53 2221.15	13 404.43	2016	2016-2017	8,01	-
414	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	54 2221.15	14 404.43	2016	2016-2017	9,32	-
415	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53 2221.15	13 404.43	2016	2016-2017	9,32	-
416	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	54 2221.15	14 404.43	2016	2016-2017	9,13	-
417	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	55 2221.15	15 404.43	2016	2016-2017	8,76	-
418	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	56 2221.15	16 404.43	2016	2016-2017	9,35	-
419	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	57 2221.15	17 404.43	2016	2016-2017	8,07	-
420	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	58 2221.15	18 404.43	2016	2016-2017	8,32	-
421	Brandenburg	rural	Maerkisch-Oderland	Falkenhagen	agricultural landscape	f	53 20.746	13 44.327	2017	2016-2017	9,50	-

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422	Brandenburg	rural	Nordwestuckermark	Arendsee	agricultural landscape	f	53 20.334	13 39.330	2017	2016-2017	9,50	-
423	Brandenburg	rural	Nordwestuckermark	Fuerstenwerder	agricultural landscape	f	53 23.302	13 35.736	2017	2016-2017	8,39	-
424	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	agricultural landscape	f	52 33.962	13 38.178	2017	2016-2017	9,63	-
425	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	m	52474314	13820982	1899	1892-1949	8,20	-
426	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	m	52474314	13820982	1899	1892-1949	8,45	-
427	Brandenburg	rural	Oder-Spree	Grunow-Dammdorf	-	m	52131509	14421513	1906	1892-1949	8,63	-
428	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	m	52557800	13036158	1909	1892-1949	8,76	-
429	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	m	52557800	13036158	1909	1892-1949	9,13	-
430	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	m	52557800	13036158	1910	1892-1949	9,03	-
431	Brandenburg	rural	Oberhavel	Borgsdorf in Hohen Neuendorf	-	m	52715814	13268077	1913	1892-1949	8,95	-
432	Brandenburg	rural	Barnim	Bernau	-	m	52696047	13550097	1919	1892-1949	8,73	-
433	Brandenburg	rural	Havelland	Brieselang	-	m	52591192	12974592	1921	1892-1949	9,16	-
434	Brandenburg	rural	Havelland	Nauen	-	m	52610488	12832286	1921	1892-1949	8,70	-
435	Brandenburg	rural	Havelland	Nauen	-	m	52610488	12832286	1921	1892-1949	8,81	-
436	Brandenburg	rural	Havelland	Brieselang	-	m	52591192	12974592	1923	1892-1949	9,01	-
437	Brandenburg	rural	Maerkisch-Oderland	Hoenow in Hoppegarten	-	m	52554418	13642433	1923	1892-1949	8,20	-
438	Brandenburg	rural	Havelland	Brieselang	-	m	52591192	12974592	1924	1892-1949	8,32	-
439	Brandenburg	rural	Havelland	Brieselang	-	m	52591192	12974592	1927	1892-1949	8,82	-
440	Brandenburg	rural	Maerkisch-Oderland	Hoenow in Hoppegarten	-	m	52554418	13642433	1928	1892-1949	8,82	-
441	Brandenburg	rural	Havelland	Bredow in Brieselang	-	m	52593443	12935718	1930	1892-1949	8,44	-
442	Brandenburg	rural	Maerkisch-Oderland	Hoenow in Hoppegarten	-	m	52554418	13642433	1930	1892-1949	7,52	7,52
443	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	m	52124574	13382056	1930	1892-1949	7,69	-
444	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	m	52124574	13382056	1930	1892-1949	8,61	-
445	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	m	52124574	13382056	1930	1892-1949	8,88	-
446	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	m	52124574	13382056	1930	1892-1949	8,32	-
447	Brandenburg	rural	Maerkisch-Oderland	Herzfelde in Ruedersdorf	-	m	52482295	13861546	1931	1892-1949	8,14	-
448	Brandenburg	rural	Dahme-Spreewald	Telz	-	m	52246352	13486311	1934	1892-1949	9,01	-
449	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	m	52557107	13885561	1934	1892-1949	8,65	-

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450	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	m	52557107	13885561	1934	1892-1949	8,63	-
451	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	m	52557107	13885561	1934	1892-1949	8,70	-
452	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	m	52557107	13885561	1934	1892-1949	8,57	-
453	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1935	1892-1949	8,82	-
454	Brandenburg	rural	Teltow-Flaeming	Sperenberg	-	m	52124574	13382056	1937	1892-1949	9,02	-
455	Brandenburg	rural	Maerkisch-Oderland	Hoenow-Mehrow in Hoppegarten	-	m	52575003	13645379	1939	1892-1949	7,70	-
456	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	m	52265221	13313631	1942	1892-1949	8,57	-
457	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	m	52265221	13313631	1942	1892-1949	8,07	-
458	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	m	52265221	13313631	1942	1892-1949	8,57	-
459	Brandenburg	rural	Teltow-Flaeming	Wietstock in Ludwigsfelde	-	m	52265221	13313631	1942	1892-1949	9,19	-
460	Brandenburg	rural	Dahme-Spreewald	Wildau	-	m	52323056	13627797	1943	1892-1949	9,13	-
461	Brandenburg	rural	Dahme-Spreewald	Wildau	-	m	52323056	13627797	1943	1892-1949	9,68	-
462	Brandenburg	rural	Dahme-Spreewald	Wildau	-	m	52323056	13627797	1943	1892-1949	8,70	-
463	Brandenburg	rural	Dahme-Spreewald	Wildau	-	m	52323056	13627797	1943	1892-1949	9,02	-
464	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	m	52557800	13036158	1943	1892-1949	8,63	-
465	Brandenburg	rural	Maerkisch-Oderland	Herzfelde in Ruedersdorf	-	m	52482295	13861546	1943	1892-1949	9,44	-
466	Brandenburg	rural	Maerkisch-Oderland	Herzfelde in Ruedersdorf	-	m	52482295	13861546	1943	1892-1949	8,82	-
467	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	m	52479641	13826682	1943	1892-1949	9,32	-
468	Brandenburg	rural	Maerkisch-Oderland	Herzfelde in Ruedersdorf	-	m	52482295	13861546	1943	1892-1949	8,76	-
469	Brandenburg	rural	Maerkisch-Oderland	Strausberg	-	m	52557107	13885561	1946	1892-1949	9,06	-
470	Brandenburg	rural	Blankenfelde-Mahlow	Juehnsdorf	-	m	52308018	13383153	1947	1892-1949	8,76	-
471	Brandenburg	rural	Blankenfelde-Mahlow	Juehnsdorf	-	m	52308018	13383153	1947	1892-1949	8,76	-
472	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	m	52677445	13373545	1949	1892-1949	9,50	-
473	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	m	52677445	13373545	1949	1892-1949	8,70	-
474	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	m	52677445	13373545	1949	1892-1949	8,76	-
475	Brandenburg	rural	Barnim	Eberswalde	-	m	52822431	13765958	1966	1957-1998	8,45	-
476	Brandenburg	rural	Barnim	Eberswalde	-	m	52822431	13765958	1966	1957-1998	8,57	-
477	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1967	1957-1998	8,32	-

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478	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel	-	m	52390323	12517421	1967	1957-1998	8,82	-
479	Brandenburg	rural	Havelland	Rathenow	-	m	52614238	12309726	1969	1957-1998	9,07	-
480	Brandenburg	rural	Havelland	Ruedersdorf	-	m	52614238	12309726	1969	1957-1998	7,75	-
481	Brandenburg	rural	Havelland	Ruedersdorf	-	m	52614238	12309726	1969	1957-1998	9,13	-
482	Brandenburg	rural	Havelland	Ruedersdorf	-	m	52614238	12309726	1969	1957-1998	8,45	-
483	Brandenburg	rural	Havelland	Ruedersdorf	-	m	52614238	12309726	1969	1957-1998	8,14	-
484	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	m	52604129	13628552	1970	1957-1998	9,13	-
485	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	m	52604129	13628552	1970	1957-1998	8,57	-
486	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	m	52604129	13628552	1970	1957-1998	8,57	-
487	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	m	52604129	13628552	1970	1957-1998	9,25	-
488	Brandenburg	rural	Dahme-Spreewald	Luckau Umgebung	-	m	51829331	13703875	1970	1957-1998	9,19	-
489	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel	-	m	52390323	12517421	1970	1957-1998	8,39	-
490	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1971	1957-1998	8,01	-
491	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1971	1957-1998	8,63	-
492	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1971	1957-1998	8,82	-
493	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1971	1957-1998	9,01	-
494	Brandenburg	rural	Potsdam-Mittelmark	Schmerzke in Brandenburg an der Havel	-	m	52380398	12583032	1971	1957-1998	8,45	-
495	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	m	52748073	13454006	1972	1957-1998	8,32	-
496	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	m	52748073	13454006	1972	1957-1998	8,76	-
497	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	m	52748073	13454006	1972	1957-1998	8,39	-
498	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	m	52748073	13454006	1972	1957-1998	8,26	-
499	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1972	1957-1998	8,76	-
500	Brandenburg	rural	Oberhavel	Schildow-Moenchmuehle	-	m	52649469	13390917	1972	1957-1998	8,63	-
501	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	m	52748073	13454006	1973	1957-1998	8,64	-
502	Brandenburg	rural	Oberhavel	Muehlenbeck Kreis Oranienburg	-	m	52677445	13373545	1973	1957-1998	8,75	-
503	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1973	1957-1998	9,07	-
504	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1973	1957-1998	8,65	-
505	Brandenburg	rural	Potsdam-Mittelmark	Ferch bei Potsdam	-	m	52303267	12913118	1973	1957-1998	8,76	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
506	Brandenburg	rural	Potsdam-Mittelmark	Ferch bei Potsdam	-	m	52303267	12913118	1973	1957-1998	8,51	-
507	Brandenburg	rural	Dahme-Spreewald	Wernsdorf Kreis Koenigs Wusterhausen, Wernsdorfer See, Protected landscape	-	m	52384542	13713457	1974	1957-1998	8,88	-
508	Brandenburg	rural	Potsdam-Mittelmark	Muehlenberg in Brandenburg an der Havel	-	m	522156	122437	1974	1957-1998	8,71	-
509	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	8,82	-
510	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	8,94	-
511	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	8,51	-
512	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	9,01	-
513	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	8,89	-
514	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	8,77	-
515	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	8,14	-
516	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	9,07	-
517	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1975	1957-1998	9,25	-
518	Brandenburg	rural	Oberhavel	Henningsdorf Kreis Oranienburg	-	m	52628647	13192213	1975	1957-1998	8,64	-
519	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1977	1957-1998	9,25	-
520	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1977	1957-1998	8,51	-
521	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1977	1957-1998	8,76	-
522	Brandenburg	rural	Maerkisch-Oderland	Hoenow-Mehrow in Hoppegarten	-	m	52575003	13645379	1978	1957-1998	8,88	-
523	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1978	1957-1998	9,32	-
524	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1978	1957-1998	8,94	-
525	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1978	1957-1998	8,81	-
526	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1978	1957-1998	8,57	-
527	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1978	1957-1998	7,58	-
528	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel, Rietzer See, natural reserve	-	m	52380060	12662780	1978	1957-1998	9,25	-
529	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel, Rietzer See, natural reserve	-	m	52380060	12662780	1978	1957-1998	8,87	-
530	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel, Rietzer See, natural reserve	-	m	52380060	12662780	1978	1957-1998	8,76	-
531	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1979	1957-1998	9,19	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
532	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1979	1957-1998	9,25	-
533	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1979	1957-1998	7,83	-
534	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1979	1957-1998	8,81	-
535	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1979	1957-1998	8,38	-
536	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1979	1957-1998	8,26	-
537	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1979	1957-1998	8,45	-
538	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1979	1957-1998	8,88	-
539	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1979	1957-1998	8,81	-
540	Brandenburg	rural	Potsdam-Mittelmark	Brandenburg an der Havel, Rietzer See, natural reserve	-	m	52380060	12662780	1979	1957-1998	9,13	-
541	Brandenburg	rural	Maerkisch-Oderland	Hoppegarten	-	m	52491872	13651215	1980	1957-1998	8,88	-
542	Brandenburg	rural	Maerkisch-Oderland	Hoppegarten	-	m	52491872	13651215	1980	1957-1998	8,39	-
543	Brandenburg	rural	Maerkisch-Oderland	Muencheberg	-	m	52515053	14075518	1980	1957-1998	8,63	-
544	Brandenburg	rural	Maerkisch-Oderland	Muencheberg	-	m	52515053	14075518	1980	1957-1998	8,50	-
545	Brandenburg	rural	Maerkisch-Oderland	Muencheberg	-	m	52515053	14075518	1980	1957-1998	9,25	-
546	Brandenburg	rural	Maerkisch-Oderland	Muencheberg	-	m	52515053	14075518	1980	1957-1998	8,88	-
547	Brandenburg	rural	Maerkisch-Oderland	Muencheberg	-	m	52515053	14075518	1980	1957-1998	8,94	-
548	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1980	1957-1998	7,78	-
549	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1980	1957-1998	9,01	-
550	Brandenburg	rural	Oder-Spree	Eisenhuettenstadt	-	m	52185350	14636756	1980	1957-1998	9,25	-
551	Brandenburg	rural	Potsdam-Mittelmark	Potsdam (surroundings)	-	m	52485625	12906010	1980	1957-1998	8,70	-
552	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1981	1957-1998	8,70	-
553	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	8,20	-
554	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1981	1957-1998	8,94	-
555	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1981	1957-1998	8,45	-
556	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1981	1957-1998	8,01	-
557	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1981	1957-1998	8,76	-
558	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1981	1957-1998	8,82	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
559	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	8,04	-
560	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	8,01	-
561	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	9,07	-
562	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	9,07	-
563	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	8,76	-
564	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	8,57	8,63
565	Brandenburg	rural	Oberhavel	Schoenfließ Kreis Oranienburg	-	m	52652879	13334172	1981	1957-1998	8,28	-
566	Brandenburg	rural	Oberhavel	Schildow, natural reserve	-	m	52630479	13356897	1981	1957-1998	7,76	-
567	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1981	1957-1998	9,31	-
568	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1981	1957-1998	8,82	-
569	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1982	1957-1998	8,94	-
570	Brandenburg	rural	Teltow-Flaeming	Sperenberg Kreis Zossen	-	m	52112979	13392356	1982	1957-1998	7,83	-
571	Brandenburg	rural	Teltow-Flaeming	Großbeeren	-	m	52357527	13316374	1982	1957-1998	9,07	8,88
572	Brandenburg	rural	Teltow-Flaeming	Großbeeren	-	m	52357527	13316374	1982	1957-1998	8,73	-
573	Brandenburg	rural	Teltow-Flaeming	Großbeeren	-	m	52357527	13316374	1982	1957-1998	9,19	-
574	Brandenburg	rural	Teltow-Flaeming	Großbeeren	-	m	52357527	13316374	1982	1957-1998	8,82	-
575	Brandenburg	rural	Barnim	Barnim	-	m	52993806	13432426	1983	1957-1998	8,32	-
576	Brandenburg	rural	Barnim	Barnim	-	m	52993806	13432426	1983	1957-1998	8,39	-
577	Brandenburg	rural	Dahme-Spreewald	Mittenwalde	-	m	52261323	13550104	1983	1957-1998	8,88	-
578	Brandenburg	rural	Dahme-Spreewald	Mittenwalde	-	m	52261323	13550104	1983	1957-1998	9,07	-
579	Brandenburg	rural	Oder-Spree	Erkner	-	m	52395934	13763690	1983	1957-1998	8,76	-
580	Brandenburg	rural	Oder-Spree	Erkner	-	m	52395934	13763690	1983	1957-1998	8,57	-
581	Brandenburg	rural	Oder-Spree	Erkner	-	m	52395934	13763690	1983	1957-1998	8,39	-
582	Brandenburg	rural	Teltow-Flaeming	Groß Machnow	-	m	52273511	13456325	1983	1957-1998	8,70	8,76
583	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1985	1957-1998	8,89	-
584	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1985	1957-1998	9,57	-
585	Brandenburg	rural	Oder-Spree	Gosen Neu-Zittau	-	m	52381753	13741069	1985	1957-1998	7,96	-
586	Brandenburg	rural	Oderspreewald-Lausitz	Großkoschen	-	m	51491792	14061458	1985	1957-1998	8,07	-
587	Brandenburg	rural	Oderspreewald-Lausitz	Großkoschen	-	m	51491792	14061458	1985	1957-1998	9,19	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
588	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1986	1957-1998	8,32	-
589	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1986	1957-1998	9,25	-
590	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1986	1957-1998	9,00	-
591	Brandenburg	rural	Maerkisch-Oderland	Lebus an der Oder	-	m	52416667	14532821	1986	1957-1998	9,25	-
592	Brandenburg	rural	Oder-Spree	Fuerstenwalde	-	m	52359633	14097266	1986	1957-1998	8,07	-
593	Brandenburg	rural	Oder-Spree	Gosen	-	m	52.389.401	13.740.425	1986	1957-1998	8,81	-
594	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	m	52623099	13608639	1988	1957-1998	8,01	-
595	Brandenburg	rural	Barnim	Oderberg	-	m	52875063	14037063	1990	1957-1998	8,01	-
596	Brandenburg	rural	Barnim	Oderberg	-	m	52875063	14037063	1990	1957-1998	5,03	-
597	Brandenburg	rural	Barnim	Oderberg	-	m	52875063	14037063	1990	1957-1998	7,70	-
598	Brandenburg	rural	Maerkisch-Oderland	Schiffmuehle near Freienwalde	-	m	52818053	14066846	1990	1957-1998	9,25	-
599	Brandenburg	rural	Maerkisch-Oderland	Schiffmuehle near Freienwalde	-	m	52818053	14066846	1990	1957-1998	8,94	-
600	Brandenburg	rural	Teltow-Flaeming	Hostfelde in Zossen	-	m	52213091	13410116	1991	1957-1998	8,88	-
601	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1993	1957-1998	8,82	-
602	Brandenburg	rural	Maerkisch-Oderland	Mallnow, natural reserve	-	m	52465122	14479306	1994	1957-1998	8,69	-
603	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	m	52474314	13820982	1994	1957-1998	9,13	-
604	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	m	52474314	13820982	1994	1957-1998	8,63	-
605	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	m	52474314	13820982	1994	1957-1998	8,88	-
606	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	53 2221.15	13 404.43	2016	2016-2017	9,01	-
607	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	54 2221.15	14 404.43	2016	2016-2017	8,51	-
608	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	55 2221.15	15 404.43	2016	2016-2017	8,39	-
609	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	56 2221.15	16 404.43	2016	2016-2017	8,20	-
610	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	57 2221.15	17 404.43	2016	2016-2017	7,76	-
611	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	58 2221.15	18 404.43	2016	2016-2017	8,32	-
612	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	59 2221.15	19 404.43	2016	2016-2017	8,51	-
613	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	60 2221.15	20 404.43	2016	2016-2017	7,64	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time period	SBL	SBL rep.
614	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	61 2221.15	21 404.43	2016	2016-2017	8,70	-
615	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	62 2221.15	22 404.43	2016	2016-2017	9,63	-
616	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	63 2221.15	23 404.43	2016	2016-2017	8,32	-
617	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	64 2221.15	24 404.43	2016	2016-2017	8,88	-
618	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	65 2221.15	25 404.43	2016	2016-2017	8,57	-
619	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	66 2221.15	26 404.43	2016	2016-2017	8,14	-
620	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	67 2221.15	27 404.43	2016	2016-2017	9,01	-
621	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	agricultural landscape	m	52 33.962	13 38.178	2017	2016-2017	9,01	-
622	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	agricultural landscape	m	53 33.962	14 38.178	2017	2016-2017	8,39	-
623	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	agricultural landscape	m	52 33.882	13 38.759	2017	2016-2017	9,44	-
624	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	agricultural landscape	m	53 33.882	14 38.759	2017	2016-2017	9,07	-

Table C Sample areas within Berlin or Brandenburg of *Harpalus rufipes* specimens with Region (urban; rural), district, Further sampling site information, Habitat if available (urban; agricultural landscape), sex (f = female; m = male), GPS coordinates (latitude; longitude), sampling year, time period, measurements of standardized body size in mm (SBL), and repeated SBL measurements in mm of a subset of specimens.

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time periode	SBL	SBL rep.
1	Berlin	urban	Charlottenburg-Wilmersdorf	Wilmersdorf	-	f	52.483.509	13.323.847	1902	1892-1949	13,81	-
2	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	f	52.423.976	13.304.580	1915	1892-1949	14,36	-
3	Berlin	urban	Pankow	Weissensee	-	f	52.551.483	13.462.153	1918	1892-1949	13,64	-
4	Berlin	urban	Spandau	Spandau	-	f	52.556.701	13.179.243	1932	1892-1949	11,81	-
5	Berlin	urban	Spandau	Spandau	-	f	52.556.701	13.179.243	1932	1892-1949	12,27	12,1
6	Berlin	urban	Marzahn-Hellersdorf	Mahldorf	-	f	52.502.296	13.616.441	1947	1892-1949	13,50	-
7	Berlin	urban	Marzahn-Hellersdorf	Mahldorf	-	f	52.502.296	13.616.441	1947	1892-1949	12,64	-
8	Berlin	urban	Marzahn-Hellersdorf	Mahldorf	-	f	52.502.296	13.616.441	1947	1892-1949	12,66	-
9	Berlin	urban	Marzahn-Hellersdorf	Mahldorf	-	f	52.502.296	13.616.441	1947	1892-1949	12,96	12,96
10	Berlin	urban	Pankow	Prenzlauer Berg	-	f	52.538.515	13.429.207	1968	1957-1998	14,17	13,89
11	Berlin	urban	Pankow	Prenzlauer Berg, Michelangelostrasse	urban	f	52.541.894	13.453.781	1969	1957-1998	13,64	13,35
12	Berlin	urban	Pankow	Weissensee	-	f	52.551.483	13.462.153	1971	1957-1998	9,97	9,83
13	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	f	52.510.052	13.559.572	1983	1957-1998	14,34	14,24
14	Berlin	urban	Treptow-Koepenik	Altglienicke, ruderal area	urban	f	52.407.085	13.549.346	1994	1957-1998	13,17	-
15	Berlin	urban	Mitte	Museum fuer Naturkunde, backyard	urban	f	52.530.377	13.379.298	2017	2016-2017	12,82	-
16	Berlin	urban	Mitte	Park am Nordbahnhof	urban	f	52,534,380	13,385,380	2017	2016-2017	12,87	-
17	Berlin	urban	Spandau	Kladow	urban	f	52,454,520	13,151,250	2017	2016-2017	13,29	-
18	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	urban	f	52,415,620	13,099,880	2017	2016-2017	12,60	-
19	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	urban	f	52,415,620	13,099,880	2017	2016-2017	12,76	-
20	Berlin	urban	Treptow-Koepenick	Mueggelheimer Forst, Strandschlossweg	urban	f	52,438,410	13,616,810	2017	2016-2017	13,78	-
21	Berlin	urban	Treptow-Koepenick	Mueggelheimer Forst, Strandschlossweg	urban	f	52,438,410	13,616,810	2017	2016-2017	13,89	-
22	Berlin	urban	Charlottenburg-Wilmersdorf	Grunewald	-	m	52.484.574	13.232.175	1901	1892-1949	12,49	-
23	Berlin	urban	Treptow-Koepenik	Treptow	-	m	52.420.743	13.687.577	1902	1892-1950	12,82	-
24	Berlin	urban	Tempelhof-Schoeneberg	Schoeneberg	-	m	52.468.257	13.353.439	1904	1892-1951	12,04	-
25	Berlin	urban	Charlottenburg-Wilmersdorf	Wilmersdorf	-	m	52.483.509	13.323.847	1905	1892-1952	13,04	-
26	Berlin	urban	Charlottenburg-Wilmersdorf	Jungfernheide	-	m	52.546.417	13.278.178	1905	1892-1953	13,13	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time periode	SBL	SBL rep.
27	Berlin	urban	Pankow	Heinersdorf	-	m	52.564.925	13.437.875	1906	1892-1954	12,95	-
28	Berlin	urban	Steglitz-Zehlendorf	Lichterfelde	-	m	52.422.301	13.294.281	1915	1892-1955	13,42	-
29	Berlin	urban	Pankow	Weissensee	-	m	52.551.483	13.462.153	1918	1892-1956	11,88	-
30	Berlin	urban	Pankow	Weissensee	-	m	52.551.483	13.462.153	1918	1892-1957	12,91	-
31	Berlin	urban	Steglitz-Zehlendorf	Lankwitz	-	m	52.431.371	13.348.350	1921	1892-1958	13,25	-
32	Berlin	urban	Spandau	Spandau	-	m	52.556.701	13.179.243	1924	1892-1959	11,41	-
33	Berlin	urban	Spandau	Spandau	-	m	52.556.701	13.179.243	1932	1892-1960	13,13	-
34	Berlin	urban	Spandau	Spandau	-	m	52.556.701	13.179.243	1932	1892-1961	11,62	-
35	Berlin	urban	Charlottenburg-Wilmersdorf	Ploetzensee in Charlottenburg Nord	-	m	52.546.897	13.326.506	1935	1892-1962	13,11	13,19
36	Berlin	urban	Reinickendorf	Reinickendorf	-	m	52.592.194	13.292.438	1936	1892-1963	13,29	-
37	Berlin	urban	Pankow	Weissensee	-	m	52.551.483	13.462.153	1946	1892-1964	10,71	-
38	Berlin	urban	Pankow	Weissensee	-	m	52.551.483	13.462.153	1946	1892-1965	13,25	-
39	Berlin	urban	Marzahn-Hellersdorf	Mahldorf	-	m	52.502.296	13.616.441	1947	1892-1966	11,51	11,55
40	Berlin	urban	Marzahn-Hellersdorf	Mahldorf	-	m	52.502.296	13.616.441	1947	1892-1967	12,43	-
41	Berlin	urban	Marzahn-Hellersdorf	Mahldorf	-	m	52.502.296	13.616.441	1947	1892-1968	13,48	-
42	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.052	13.559.572	1967	1957-1998	12,33	-
43	Berlin	urban	Pankow	Prenzlauer Berg	-	m	52.538.515	13.429.207	1968	1957-1998	13,09	12,88
44	Berlin	urban	Marzahn-Hellersdorf	Biesdorf	-	m	52.510.052	13.559.572	1969	1957-1998	12,49	12,6
45	Berlin	urban	Reinickendorf	Tegel	-	m	52.596.216	13.280.867	1978	1957-1998	13,13	-
46	Berlin	urban	Reinickendorf	Tegel	-	m	52.596.216	13.280.867	1978	1957-1998	13,63	-
47	Berlin	urban	Reinickendorf	Wittenau, garden plot	urban	m	52.593.839	13.311.081	1979	1957-1998	12,15	12,45
48	Berlin	urban	Reinickendorf	Wittenau, garden plot	urban	m	52.593.839	13.311.081	1988	1957-1998	13,29	-
49	Berlin	urban	Reinickendorf	Wittenau, garden plot	urban	m	52.593.839	13.311.081	1988	1957-1998	12,56	-
50	Berlin	urban	Reinickendorf	Wittenau, garden plot	urban	m	52.593.839	13.311.081	1988	1957-1998	13,67	-
51	Berlin	urban	Treptow-Koepenik	Treptow	-	m	52.420.743	13.687.577	1993	1957-1998	12,56	12,74
52	Berlin	urban	Mitte	Park at Nordbahnhof	urban	m	52,534,380	13,385,380	2017	2016-2017	11,18	-
53	Berlin	urban	Mitte	Park at Nordbahnhof	urban	m	52,534,380	13,385,380	2017	2016-2017	11,76	-
54	Berlin	urban	Mitte	Tiergarten	urban	m	52,514,260	13,375,760	2017	2016-2017	10,99	-
55	Berlin	urban	Pankow	Buch	urban	m	52,630,440	13,484,280	2017	2016-2017	11,26	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time periode	SBL	SBL rep.
56	Berlin	urban	Pankow	Buch	urban	m	52,630,440	13,484,280	2017	2016-2017	10,71	-
57	Berlin	urban	Reinickendorf	Tegeler Forst, Tegeler See	urban	m	52,582,650	13,247,260	2017	2016-2017	10,67	-
58	Berlin	urban	Reinickendorf	Tegeler Forst, Tegeler See	urban	m	52,582,650	13,247,260	2017	2016-2017	11,76	-
59	Berlin	urban	Spandau	Kladow	urban	m	52,454,520	13,151,250	2017	2016-2017	12,64	-
60	Berlin	urban	Spandau	Kladow	urban	m	52,454,520	13,151,250	2017	2016-2017	13,03	-
61	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	urban	m	52,415,620	13,099,880	2017	2016-2017	12,58	-
62	Berlin	urban	Treptow-Koepenick	Adlershof, Fritz Lesch Sportplatz	urban	m	52,439,550	13,555,840	2017	2016-2017	12,15	-
63	Brandenburg	rural	Oberhavel	Sonnenberg bei Gransee	-	f	52.994.294	13.076.189	1892	1892-1949	12,50	-
64	Brandenburg	rural	Havelland	Nauen	-	f	52.597.978	13.076.190	1910	1892-1949	13,52	-
65	Brandenburg	rural	Havelland	Nauen	-	f	52.597.978	13.076.191	1910	1892-1949	13,35	-
66	Brandenburg	rural	Havelland	Brieselang	-	f	52.591.817	13.076.192	1924	1892-1949	12,99	-
67	Brandenburg	rural	Havelland	Brieselang	-	f	52.591.817	13.076.193	1924	1892-1949	13,09	-
68	Brandenburg	rural	Havelland	Nauen	-	f	52.597.978	13.076.194	1924	1892-1949	11,98	-
69	Brandenburg	rural	Havelland	Nauen	-	f	52.597.978	13.076.195	1927	1892-1949	14,05	-
70	Brandenburg	rural	Havelland	Brieselang	-	f	52.591.817	13.076.196	1942	1892-1949	11,61	-
71	Brandenburg	rural	Havelland	Finkenkrug in Falkensee	-	f	52.560.357	13.076.197	1942	1892-1949	13,68	13,91
72	Brandenburg	rural	Barnim	Roentgental	-	f	52.644.123	13.076.198	1946	1892-1949	14,17	-
73	Brandenburg	rural	Barnim	Wandlitz Kreis Bernau	-	f	52.756.385	13.076.199	1972	1957-1998	14,07	13,95
74	Brandenburg	rural	Dahme-Spreewald	Koenigs Wusterhausen, Wernsdofer See, natural reserve	-	f	52.385.459	13.076.200	1974	1957-1998	12,51	12,35
75	Brandenburg	rural	Dahme-Spreewald	Koenigs Wusterhausen, Wernsdofer See, natural reserve	-	f	52.385.459	13.076.201	1977	1957-1998	13,56	-
76	Brandenburg	rural	Dahme-Spreewald	Koenigs Wusterhausen, Wernsdofer See, natural reserve	-	f	52.385.459	13.076.202	1980	1957-1998	13,72	13,91
77	Brandenburg	rural	Oder-Spree	Frankfurt an der Oder (Bezirk)	-	f	52.272.963	13.076.203	1980	1957-1998	12,95	-
78	Brandenburg	rural	Teltow-Flaeming	Kallinchen in Zossen	-	f	52.209.976	13.076.204	1981	1957-1998	15,21	-
79	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	13,78	-

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80	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	13,52	-
81	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	12,84	-
82	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	14,05	-
83	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	14,11	-
84	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	14,25	-
85	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	12,31	-
86	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	13,91	-
87	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	12,24	-
88	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	f	53.222.115	13.404.430	2016	2016-2017	13,39	-
89	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	12,50	-
90	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,25	-
91	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	14,17	-
92	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	12,70	-
93	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,85	-
94	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	12,64	-
95	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,56	-
96	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,03	-
97	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	14,21	-
98	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,70	-
99	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	14,11	-
100	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	14,01	-
101	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,78	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time periode	SBL	SBL rep.
102	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,29	-
103	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,46	-
104	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,19	-
105	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,46	-
106	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	12,95	-
107	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,78	-
108	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	14,54	-
109	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,46	-
110	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,72	-
111	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	14,28	-
112	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,81	-
113	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,82	-
114	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	14,36	-
115	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,66	-
116	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,46	-
117	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,44	-
118	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	12,78	-
119	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,27	-
120	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	13,64	-
121	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	f	52.535.274	13.802.022	2017	2016-2017	12,86	-
122	Brandenburg	rural	Nordwestuckermark	Arendsee	agricultural landscape	f	53.203.340	13.393.300	2017	2016-2017	13,52	-
123	Brandenburg	rural	Nordwestuckermark	Fuerstenwerder	agricultural landscape	f	53.233.020	13.357.360	2017	2016-2017	13,35	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time periode	SBL	SBL rep.
124	Brandenburg	rural	Nordwestuckermark	Arendsee	agricultural landscape	f	53.203.340	13.393.300	2017	2016-2017	11,84	-
125	Brandenburg	rural	Oberhavel	Sonnenberg bei Gransee	-	m	52.991.194	13.063.486	1892	1892-1949	13,17	-
126	Brandenburg	rural	Havelland	Finkenkrug	-	m	52.560.357	13.035.643	1909	1892-1949	12,20	-
127	Brandenburg	rural	Havelland	Nauen	-	m	52.601.980	12.868.698	1910	1892-1949	12,66	-
128	Brandenburg	rural	Maerkisch-Oderland	Ruedersdorf	-	m	52.479.423	13.824.658	1910	1892-1949	12,31	-
129	Brandenburg	rural	Maerkisch-Oderland	Heidekrug bei Muencheberg	-	m	52.477.059	13.958.988	1912	1892-1949	11,51	-
130	Brandenburg	rural	Maerkisch-Oderland	Heidekrug bei Muencheberg	-	m	52.477.059	13.958.988	1912	1892-1949	11,88	-
131	Brandenburg	rural	Uckermark	Malchow	-	m	53.465.255	12.432.494	1919	1892-1949	13,07	-
132	Brandenburg	rural	Havelland	Brieselang	-	m	52.591.817	13.006.864	1924	1892-1949	12,20	-
133	Brandenburg	rural	Havelland	Brieselang	-	m	52.591.817	13.006.864	1924	1892-1949	12,43	-
134	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	-	m	52.322.826	13.414.444	1927	1892-1949	12,60	-
135	Brandenburg	rural	Teltow-Flaeming	Blankenfelde-Mahlow	-	m	52.322.826	13.414.444	1927	1892-1949	12,88	-
136	Brandenburg	rural	Barnim	Glambeck in Friedrichswalde	-	m	53.023.489	13.821.411	1929	1892-1949	13,05	-
137	Brandenburg	rural	Havelland	Nauen	-	m	52.597.978	12.832.286	1942	1892-1949	11,61	-
138	Brandenburg	rural	Havelland	Nauen	-	m	52.597.978	12.832.286	1942	1892-1949	12,33	-
139	Brandenburg	rural	Havelland	Nauen	-	m	52.597.978	12.832.286	1942	1892-1949	12,47	-
140	Brandenburg	rural	Havelland	Brieselang	-	m	52.591.817	13.006.864	1942	1892-1949	10,28	-
141	Brandenburg	rural	Oder-Spree	Dubrow in Muellrose	-	m	52.272.540	14.388.287	1953		12,99	-
142	Brandenburg	rural	Barnim	Wandlitz, Lottschesee	-	m	52.811.359	13.501.632	1968	1957-1998	11,30	-
143	Brandenburg	rural	Barnim	Wandlitz, Lottschesee	-	m	52.811.359	13.501.632	1968	1957-1998	13,13	-
144	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	m	52.622.578	13.607.609	1970	1957-1998	13,15	12,99
145	Brandenburg	rural	Dahme-Spreewald	Koenigs Wusterhausen, Wernsdofer See, natural reserve	-	m	52.385.459	13.710.324	1974	1957-1998	12,29	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time periode	SBL	SBL rep.
146	Brandenburg	rural	Dahme-Spreewald	Koenigs Wusterhausen, Wernsdofer See, natural reserve	-	m	52.385.459	13.710.324	1974	1957-1998	11,41	11,45
147	Brandenburg	rural	Barnim	Blumberg in Ahrensfelde	-	m	52.622.578	13.607.609	1975	1957-1998	11,69	-
148	Brandenburg	rural	Dahme-Spreewald	Koenigs Wusterhausen, Wernsdofer See, natural reserve	-	m	52.385.459	13.710.324	1985	1957-1998	12,90	-
149	Brandenburg	rural	Potsdam-Mittelmark	Deetz	-	m	52.436.946	12.765.549	1992	1957-1998	12,53	12,53
150	Brandenburg	rural	Maerkisch-Oderland	Mallnow in Lebus	-	m	52.459.265	14.482.911	1993	1957-1998	11,80	12,17
151	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	53.222.115	13.404.430	2016	2016-2017	12,53	-
152	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	53.222.115	13.404.430	2016	2016-2017	11,22	-
153	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	54.222.115	14.404.430	2016	2016-2017	12,47	-
154	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	55.222.115	15.404.430	2016	2016-2017	12,92	-
155	Brandenburg	rural	Uckermark	Nordwest Uckermark	agricultural landscape	m	56.222.115	16.404.430	2016	2016-2017	12,00	-
156	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,50	-
157	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	13,07	-
158	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,64	-
159	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	13,19	-
160	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,41	-
161	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	13,09	-
162	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,14	-
163	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,08	-
164	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,70	-
165	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	13,17	-
166	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	13,25	-
167	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,90	-

ID	Area	Region	District	Further sampling site information	Habitat	Sex	Latitude	Longitude	Year	Time periode	SBL	SBL rep.
168	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,31	-
169	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	13,25	-
170	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,82	-
171	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,72	-
172	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,76	-
173	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,37	-
174	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,41	-
175	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,90	-
176	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	12,64	-
177	Brandenburg	rural	Maerkisch-Oderland	Fredersdorf-Vogeldorf	agricultural landscape	m	52.535.274	13.802.022	2017	2016-2017	13,13	-
178	Brandenburg	rural	Nordwestuckermark	Arendsee	agricultural landscape	m	53.203.340	13.393.300	2017	2016-2017	11,71	-
179	Brandenburg	rural	Nordwestuckermark	Fuerstenwerder	agricultural landscape	m	53.233.020	13.357.360	2017	2016-2017	11,80	-
180	Brandenburg	rural	Nordwestuckermark	Fuerstenwerder	agricultural landscape	m	54.233.020	14.357.360	2017	2016-2017	10,69	-

Table D1 Nitrogen and Carbon stable isotope measurements of *Harpalus affinis*' legs with sex (m = male; f = female), sampling region (Berlin; Brandenburg), habitat (urban; agricultural landscape), sampling district, further sampling site information, GPS coordinates (latitude; longitude), sampling year. Measurements of stable isotopes with weight of leg tissue in mg (weight), delta $^{15}N/^{14}N$ values (d 15 N / 14 N), mg of nitrogen per sample (mg N / sample), amount of nitrogen in % (% N), delta $^{13}C/^{12}C$ values (d 13 C / 12 C), mg of nitrogen per sample (mg C / sample), amount of carbon in % (% C).

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Legs						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
1	m	Berlin	urban	Treptow-Koepenick	Krummendammer Heide	52,46215	13,63198	2017	1,426	2,569	0,164	11,519	-27,038	0,706	49,520
2	m	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	0,619	3,278	0,063	10,162	-26,267	0,337	54,409
3	m	Berlin	urban	Tempelhof-Schoeneberg	Park am Gleisdreieck, Flaschenhalspark	52,48854	13,37276	2017	0,868	1,212	0,102	11,704	-20,717	0,445	51,272
4	m	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	0,698	2,761	0,075	10,816	-25,621	0,350	50,155
5	m	Berlin	urban	Mitte	Tiergarten	52,51451	13,37353	2017	1,478	3,076	0,166	11,217	-26,359	0,743	50,296
6	f	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	0,900	-1,925	0,103	11,460	-24,951	0,451	50,065
7	f	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	52,47541	13,40603	2017	1,361	4,111	0,159	11,650	-26,156	0,700	51,449
8	f	Berlin	urban	Charlottenburg-Wilmersdorf	Grunewald, Am Postfenn	52,50058	13,22444	2017	0,801	-0,308	0,082	10,204	-26,941	0,359	44,879
9	f	Berlin	urban	Treptow-Koepenick	AS Stubenrauchstrasse	52,43429	13,49902	2017	1,287	5,394	0,137	10,659	-26,86	0,700	54,371
10	f	Berlin	urban	Pankow	Karow	52,61662	13,44811	2017	1,242	3,725	0,132	10,650	-26,56	0,687	55,340
11	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,063	4,836	0,094	8,805	-26,962	0,565	53,135
12	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,988	5,657	0,092	9,278	-26,31	0,380	38,486
13	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	1,340	8,162	0,157	11,719	-25,82	0,689	51,441
14	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	0,829	-2,988	0,095	11,471	-22,423	0,440	53,065
15	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	1,647	6,682	0,191	11,577	-26,868	0,841	51,034
16	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,202	5,808	0,142	11,852	-26,836	0,609	50,631
17	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,239	7,489	0,147	11,878	-25,578	0,636	51,355
18	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,168	6,392	0,138	11,796	-27,448	0,600	51,386

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Legs						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
19	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,792	6,376	0,090	11,399	-22,806	0,406	51,226
20	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,670	7,734	0,079	11,820	-26,291	0,343	51,205

Table D2 Nitrogen and Carbon stable isotope measurements of *Harpalus affinis*' cuticula with sex (m = male; f = female), sampling region (Berlin; Brandenburg), habitat (urban; agricultural landscape), sampling district, further sampling site information, GPS coordinates (latitude; longitude), sampling year. Measurements of stable isotopes with weight of cuticula tissue in mg (weight), delta $^{15}N/^{14}N$ values (d 15 N / 14 N), mg of nitrogen per sample (mg N / sample), amount of nitrogen in % (% N), delta $^{13}C/^{12}C$ values (d 13 C / 12 C), mg of nitrogen per sample (mg C / sample), amount of carbon in % (% C).

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Cuticula						
									weight	d 15 N / 14 N	Mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
1	m	Berlin	urban	Treptow-Koepenick	Krummendammer Heide	52,46215	13,63198	2017	1,524	3,149	0,163	10,713	-26,785	0,757	49,650
2	m	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	1,361	2,479	0,139	10,242	-26,161	0,719	52,809
3	m	Berlin	urban	Tempelhof-Schoeneberg	Park am Gleisdreieck, Flaschenhalspark	52,48854	13,37276	2017	0,638	0,639	0,068	10,614	-22,118	0,326	51,079
4	m	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	1,142	2,663	0,119	10,416	-25,68	0,576	50,472
5	m	Berlin	urban	Mitte	Tiergarten	52,51451	13,37353	2017	1,497	3,015	0,152	10,137	-26,46	0,802	53,586
6	f	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	0,749	-2,438	0,079	10,497	-25,542	0,391	52,242
7	f	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	52,47541	13,40603	2017	1,347	4,157	0,143	10,612	-25,578	0,710	52,726
8	f	Berlin	urban	Charlottenburg-Wilmersdorf	Grunewald, Am Postfenn	52,50058	13,22444	2017	0,745	-0,906	0,078	10,455	-27,353	0,393	52,759
9	f	Berlin	urban	Treptow-Koepenick	AS Stubenrauchstrasse	52,43429	13,49902	2017	0,967	5,532	0,102	10,521	-26,539	0,526	54,424
10	f	Berlin	urban	Pankow	Karow	52,61662	13,44811	2017	0,978	6,100	0,099	10,112	-26,772	0,535	54,734
11	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,310	4,169	0,122	9,346	-25,869	0,714	54,491
12	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,962	7,209	0,156	16,201	-25,949	0,761	79,157
13	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	1,448	5,886	0,107	7,395	-26,106	0,466	32,157
14	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	0,917	-3,168	0,096	10,429	-26,671	0,493	53,730
15	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	1,278	6,440	0,133	10,370	-26,774	0,667	52,204
16	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	0,944	6,623	0,105	11,120	-26,803	0,487	51,541
17	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,016	7,176	0,113	11,102	-25,68	0,541	53,205

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Cuticula						
									weight	d 15 N / 14 N	Mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
18	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,109	6,126	0,123	11,077	-28,03	0,583	52,597
19	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,392	7,380	0,137	9,818	-23,76	0,782	56,143
20	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,885	4,291	0,090	10,196	-26,923	0,483	54,535

Table D3 Nitrogen and Carbon stable isotope measurements of *Harpalus affinis*' muscles with sex (m = male; f = female), sampling region (Berlin; Brandenburg), habitat (urban; agricultural landscape), sampling district, further sampling site information, GPS coordinates (latitude; longitude), sampling year. Measurements of stable isotopes with weight of muscles tissue in mg (weight), delta $^{15}N/^{14}N$ values (d 15 N / 14 N), mg of nitrogen per sample (mg N / sample), amount of nitrogen in % (% N), delta $^{13}C/^{12}C$ values (d 13 C / 12 C), mg of nitrogen per sample (mg C / sample), amount of carbon in % (% C).

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Muscles						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
1	m	Berlin	urban	Treptow-Koepenick	Krummendammer Heide	52,46215	13,63198	2017	-	-	-	-	-	-	-
2	m	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	0,137	5,082	0,014	10,266	-25,130	0,067	48,990
3	m	Berlin	urban	Tempelhof-Schoeneberg	Park am Gleisdreieck, Flaschenhalspark	52,48854	13,37276	2017	0,157	4,164	0,021	13,103	-25,869	0,078	49,614
4	m	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	-	-	-	-	-	-	-
5	m	Berlin	urban	Mitte	Tiergarten	52,51451	13,37353	2017	0,625	4,534	0,066	10,529	-25,686	0,321	51,334
6	f	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	0,158	1,605	0,017	10,680	-22,077	0,071	44,804
7	f	Berlin	urban	Tempelhof-Schoeneberg	Tempelhofer Feld	52,47541	13,40603	2017	0,419	6,754	0,041	9,856	-26,597	0,183	43,761
8	f	Berlin	urban	Charlottenburg-Wilmersdorf	Grunewald, Am Postfenn	52,50058	13,22444	2017	-	-	-	-	-	-	-
9	f	Berlin	urban	Treptow-Koepenick	AS Stubenrauchstrasse	52,43429	13,49902	2017	-	-	-	-	-	-	-
10	f	Berlin	urban	Pankow	Karow	52,61662	13,44811	2017	-	-	-	-	-	-	-
11	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,478	6,484	0,048	10,009	-26,963	0,255	53,362
12	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,482	5,538	0,053	10,916	-25,723	0,240	49,783
13	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	0,346	9,172	0,046	13,294	-25,282	0,161	46,594
14	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	0,552	-0,479	0,067	12,202	-23,769	0,279	50,611
15	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	0,413	8,222	0,055	13,272	-25,757	0,204	49,478
16	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	0,48	7,365	0,064	13,305	-26,302	0,231	48,215
17	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	0,422	8,367	0,057	13,537	-25,543	0,204	48,255

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Muscles						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
18	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,234	5,333	0,030	12,612	-25,662	0,121	51,881
19	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	-	-	-	-	-	-	-
20	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	-	-	-	-	-	-	-

Table D4 Nitrogen and Carbon stable isotope measurements of *Harpalus rufipes*' legs with sex (m = male; f = female), sampling region (Berlin; Brandenburg), habitat (urban; agricultural landscape), sampling district, further sampling site information, GPS coordinates (latitude; longitude), sampling year. Measurements of stable isotopes with weight of leg tissue in mg (weight), delta $^{15}N/^{14}N$ values (d 15 N / 14 N), mg of nitrogen per sample (mg N / sample), amount of nitrogen in % (% N), delta $^{13}C/^{12}C$ values (d 13 C / 12 C), mg of nitrogen per sample (mg C / sample), amount of carbon in % (% C).

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Legs						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
21	f	Berlin	urban	Treptow-Koepenick	Mueggelheimer Forst, Strandschlossweg	52,43841	13,61681	2017	1,436	3,508	0,133	9,268	-33,521	0,810	56,421
22	f	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	1,382	2,96	0,152	11,011	-27,111	0,723	52,288
23	f	Berlin	urban	Mitte	Park am Nordbahnhof	52,53438	13,38538	2017	1,750	7,365	0,192	10,947	-14,086	0,884	50,511
24	f	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	1,336	2,418	0,150	11,231	-23,952	0,683	51,093
25	f	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,414	5,53	0,114	8,077	-28,11	0,779	55,098
26	m	Berlin	urban	Reinickendorf	Tegeler Forst, Tegeler See	52,58265	13,24726	2017	0,760	8,029	0,086	11,271	-28,194	0,370	48,663
27	m	Berlin	urban	Pankow	Buch	52,63044	13,48428	2017	1,601	8,262	0,185	11,552	-25,576	0,805	50,300
28	m	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,355	5,422	0,156	11,531	-27,646	0,690	50,932
29	m	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	1,228	2,632	0,140	11,417	-27,132	0,614	49,986
30	m	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,237	5,186	0,139	11,267	-27,156	0,626	50,618
31	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	1,020	7,75	0,115	11,286	-25,327	0,498	48,848
32	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	1,858	8,123	0,214	11,518	-24,412	0,915	49,269
33	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	1,617	7,973	0,177	10,938	-19,796	0,824	50,960
34	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,879	7,015	0,222	11,796	-27,763	0,944	50,217
35	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,662	5,599	0,197	11,830	-16,437	0,853	51,341
36	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	2,107	8,876	0,243	11,514	-28,275	1,101	52,231
37	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,720	5,644	0,204	11,850	-27,166	0,890	51,755
38	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,860	6,421	0,217	11,675	-27,396	0,983	52,855

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Legs						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
39	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,062	6,279	0,124	11,699	-21,219	0,543	51,100
40	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222225	13404430	2016	0,940	6,409	0,108	11,521	-18,511	0,454	48,341

Table D5 Nitrogen and Carbon stable isotope measurements of *Harpalus rufipes*' cuticula with sex (m = male; f = female), sampling region (Berlin; Brandenburg), habitat (urban; agricultural landscape), sampling district, further sampling site information, GPS coordinates (latitude; longitude), sampling year. Measurements of stable isotopes with weight of cuticula tissue in mg (weight), delta $^{15}N/^{14}N$ values (d 15 N / 14 N), mg of nitrogen per sample (mg N / sample), amount of nitrogen in % (% N), delta $^{13}C/^{12}C$ values (d 13 C / 12 C), mg of nitrogen per sample (mg C / sample), amount of carbon in % (% C).

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Cuticula						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
21	f	Berlin	urban	Treptow-Koepenick	Mueggelheimer Forst, Strandschlossweg	52,43841	13,61681	2017	1,692	3,215	0,137	8,105	-33,072	0,977	57,723
22	f	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	0,935	2,853	0,098	10,459	-26,802	0,458	48,956
23	f	Berlin	urban	Mitte	Park am Nordbahnhof	52,53438	13,38538	2017	1,774	7,507	0,152	8,558	-15,827	0,998	56,2432356
24	f	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	1,401	3,286	0,147	10,460	-24,249	0,697	49,749
25	f	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,410	5,260	0,107	7,555	-27,923	0,802	56,906
26	m	Berlin	urban	Reinickendorf	Tegeler Forst, Tegeler See	52,58265	13,24726	2017	1,018	2,871	0,097	9,528	-28,849	0,528	51,867
27	m	Berlin	urban	Pankow	Buch	52,63044	13,48428	2017	1,293	8,167	0,134	10,334	-25,084	0,643	49,763
28	m	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,234	5,676	0,110	8,954	-28,11	0,664	53,848
29	m	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	1,075	3,143	0,115	10,713	-26,54	0,553	51,422
30	m	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,197	5,413	0,116	9,702	-27,236	0,590	49,292
31	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	1,365	7,737	0,145	10,588	-25,483	0,684	50,129
32	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	1,752	8,557	0,189	10,777	-23,961	0,887	50,651
33	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	1,526	7,908	0,166	10,870	-26,026	0,777	50,904
34	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,659	5,835	0,182	11,000	-28,171	0,844	50,863
35	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,549	6,739	0,164	10,590	-18,501	0,776	50,080
36	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	1,726	8,850	0,182	10,550	-28,894	0,894	51,811
37	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,681	5,125	0,174	10,327	-26,87	0,878	52,242

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Cuticula						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
38	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,406	5,370	0,140	9,976	-27,474	0,751	53,383
39	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,020	6,340	0,107	10,523	-22,019	0,513	50,296
40	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222225	13404430	2016	1,473	5,576	0,155	10,527	-19,222	0,754	51,217

Table D6 Nitrogen and Carbon stable isotope measurements of *Harpalus rufipes*' muscles with sex (m = male; f = female), sampling region (Berlin; Brandenburg), habitat (urban; agricultural landscape), sampling district, further sampling site information, GPS coordinates (latitude; longitude), sampling year. Measurements of stable isotopes with weight of muscle tissue in mg (weight), delta $^{15}N/^{14}N$ values (d 15 N / 14 N), mg of nitrogen per sample (mg N / sample), amount of nitrogen in % (% N), delta $^{13}C/^{12}C$ values (d 13 C / 12 C), mg of nitrogen per sample (mg C / sample), amount of carbon in % (% C).

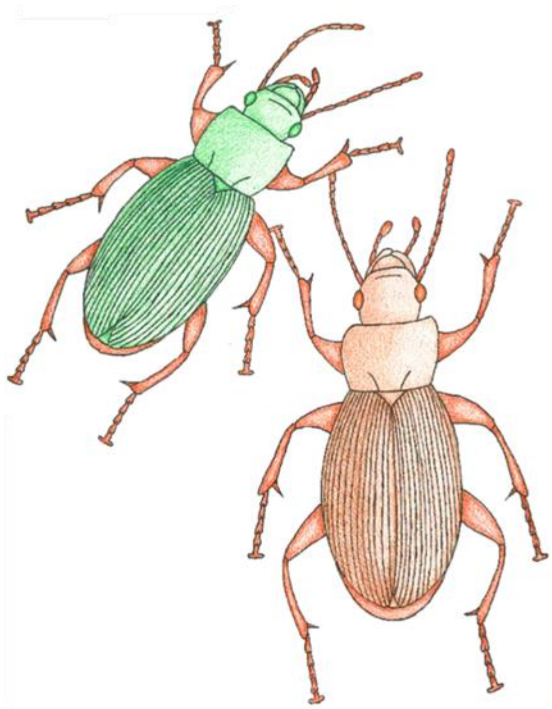
No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Muscles						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
21	f	Berlin	urban	Treptow-Koepenick	Mueggelheimer Forst, Strandschlossweg	52,43841	13,61681	2017	0,378	2,807	0,029	7,549	-32,459	0,198	52,334
22	f	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	1,243	2,673	0,139	11,191	-27,115	0,656	52,798
23	f	Berlin	urban	Mitte	Park am Nordbahnhof	52,53438	13,38538	2017	0,528	7,942	0,038	7,221	-16,344	0,246	46,614
24	f	Berlin	urban	Steglitz-Zehlendorf	Dueppeler Forst, Schloss Glienicke	52,41562	13,09988	2017	1,493	3,132	0,143	9,552	-24,537	0,612	41,022
25	f	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	0,321	6,043	0,015	4,687	-26,444	0,094	29,295
26	m	Berlin	urban	Reinickendorf	Tegeler Forst, Tegeler See	52,58265	13,24726	2017	0,834	3,038	0,030	3,656	-28,005	0,139	16,709
27	m	Berlin	urban	Pankow	Buch	52,63044	13,48428	2017	0,434	8,777	0,054	12,443	-24,589	0,203	46,793
28	m	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,115	5,660	0,108	9,698	-27,985	0,609	54,620
29	m	Berlin	urban	Mitte	Tiergarten	52,51426	13,37576	2017	0,509	4,601	0,066	12,954	-25,195	0,239	46,864
30	m	Berlin	urban	Spandau	Kladow	52,45452	13,15125	2017	1,369	5,504	0,159	11,583	-26,538	0,676	49,407
31	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	0,655	8,845	0,084	12,843	-24,862	0,311	47,522
32	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Falkenhagen	53207460	13443270	2017	0,948	8,452	0,111	11,663	-24,223	0,406	42,796
33	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	0,470	7,558	0,057	12,197	-25,314	0,210	44,780
34	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,749	7,167	0,083	11,019	-26,929	0,290	38,739
35	f	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	1,100	7,836	0,142	12,882	-17,743	0,541	49,154
36	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Guestow	53206110	13459430	2017	0,625	9,265	0,076	12,195	-27,318	0,291	46,542
37	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	0,918	6,244	0,118	12,841	-26,333	0,450	49,062
38	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Arendsee	53203340	13393300	2017	1,024	7,464	0,036	3,552	-26,307	0,144	14,105

No	Sex	Region	Habitat	District	Further sampling site information	Latitude	Longitude	Year	Muscles						
									weight	d 15 N / 14 N	mg N / sample	% N	d 13 C / 12 C	mg C / sample	% C
39	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222115	13404430	2016	0,362	7,254	0,046	12,611	-22,557	0,167	46,096
40	m	Brandenburg	agricultural landscape	Nordwest Uckermark	Basedow, Prenzlau	53222225	13404430	2016	1,169	7,556	0,148	12,662	-21,741	0,545	46,639

6.3 Supplementary material: Paper 3

Spatio-temporal color differences between urban and rural populations of a ground beetle during the last 100 years

Keinath, S., Frisch, J., Müller, J., Mayer, F., and Rödel, M.-O. (2020). *Spatio-temporal color differences between urban and rural populations of a ground beetle during the last 100 years*. Frontiers in Ecology and Evolution – Urban Ecology, 7, Art. 525. https://doi.org/10.3389/fevo.2019.00525.



Appendix A: Sample areas within Berlin or Brandenburg with districts, types of regions, habitats (if assessable) and GPS coordinates of 546 *Harpalus affinis* specimens from the collections of the Museum für Naturkunde, Berlin and 114 recently collected specimens, spanning the times from 1892 to 2017, including 267 females and 393 males.

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
16	Berlin	Altglienicke, Ruderal area	Urban	Urban	1993	52 2442.33	13.3237.36
3	Berlin	Berlin-Mitte	Urban	Urban	1901	52 320.67	13 2331.95
1	Berlin	Berlin-Mitte, Tiergarten	Urban	Urban	2017	52 51.426	13 37.576
13	Berlin	Biesdorf	Urban	-	1966; 1967; 1969; 1975; 1979	51 302641	13 342059
10	Berlin	Biesdorf, Rubble mountain	Urban	-	1969	52 2944.66	13 3527.70
2	Berlin	Pankow, Buch	Urban	-	1919	13 48.428	52 63.044
1	Berlin	Friedrichsfelde, Tierpark	Urban	Urban	1971	52 306.87	13 3151.70
2	Berlin	Friedrichshagen, Meadow	Urban	-	1978	52 274.95	13 3636.87
1	Berlin	Friedrichshain-Kreuzberg, Pankow, Lichtenberg, Marzahn-Hellersdorf, Landsberger Allee	Urban	Urban	1987	52 326.32	13 3041.27
1	Berlin	Gosen, Wernsdorfer See	Urban	-	1986	52 232.97	13 4213.67
22	Berlin	Gruenau	Urban	-	1906; 1907; 1909	52 2411.75	13 3534.30

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
16	Berlin	Hellersdorf, Kienberg	Urban	-	1986; 1987	52 324.71	13 3452.95
3	Berlin	Hellersdorf, Sewage farm	Urban	Urban	1968	52 3452.64	13 335.63
1	Berlin	Hohenschoenhausen	Urban	-	1987	52 335.88	13 2938.45
3	Berlin	Johannistal, Ruderal area	Urban	Urban	1993; 1994	52 2616.88	13 3047.05
2	Berlin	Kaulsdorf	Urban	-	1943; 1972	52 301.06	13 3519.13
1	Berlin	Kaulsdorf, Schuttplatte	Urban	-	1968	52 2842.30	13 3438.87
1	Berlin	Koepenick, Railroad embankment Wuhlheide	Urban	Urban	1972	52 2716.65	13 3332.38
2	Berlin	Lichtenberg, Fennpfuhl	Urban	-	1975	52 3139.97	13 2829.75
2	Berlin	Lichtenberg, Landsberger Allee	Urban	Urban	1976	52 321.76	13 2947.67
5	Berlin	Lichtenberg, Malchower See	Urban	-	1977; 1980	52 3420.69	13 2915.29
2	Berlin	Lichtenberg, Rummelsburg	Urban	-	1976	52 2956.85	13 2911.37
2	Berlin	Lichtenrade	Urban	-	1909	52 2410.02	13 229.71
10	Berlin	Lichterfelde, Groß Lichterfelde	Urban	-	1904; 1908; 1915	52 2531.10	13 1854.76

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
19	Berlin	Mahlsdorf	Urban	-	1947; 1992	52 3010.24	13 3612.61
3	Berlin	Marienfelde, Dumpsite	Urban	-	1971; 1980	52 2448.77	13 2312.55
4	Berlin	Marienfelde, Meadow	Urban	-	1973	52 2420.53	13 222.28
2	Berlin	Neukoelln, Ruderal area	Urban	Urban	1993	52 2541.76	13 2540.11
1	Berlin	Neukoelln, Sports field	Urban	Urban	1994	52 2541.71	13 2324.78
4	Berlin	Pankow	Urban	-	1977	52 3526.50	13 2554.12
1	Berlin	Pankow, Blankenburg	Urban	-	1994	52 63.390	13 39.376
6	Berlin	Pankow, Heinersdorf	Urban	-	1977; 1979	52 3354.21	13 2555.86
1	Berlin	Pankow, Niederschoenhausen	Urban	-	1977	52 351.06	13 2420.87
41	Berlin	Prenzlauer Berg, Oderbruchberg	Urban	-	1908; 1968; 1969; 1970; 1972; 1975; 1980	52 329.74	13 2743.16
1	Berlin	Reinickendorf, Luebras, Dumpsite	Urban	Urban	1981	52 3654.25	13 2146.76

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
9	Berlin	Reinickendorf, Wittenau, Garden plot	Urban	Urban	1979; 1981; 1984; 1988	52 3532.84	13 1946.90
2	Berlin	Spandau	Urban	-	1901	52 326.67	13 121.07
1	Berlin	Spandau, Flur Seeburg	Urban	-	1934	52 3121.86	13 1035.68
4	Berlin	Spandau, Hahneberg	Urban	-	1993	52 3118.00	13 815.00
1	Berlin	Staaken, Spandau	Urban	-	1937	52 327.12	13 831.28
1	Berlin	Steglitz	Urban	-	1906	52 2722.92	13 1956.99
1	Berlin	Tempelhof, Felixstraße	Urban	Urban	1957	52 2746.75	13 2340.18
8	Berlin	Treptow	Urban	-	1902; 1909	52 2513.28	13 3712.08
1	Berlin	Treptow, Ruderal area	Urban	Urban	1993; 1994	52 2754.03	13 3319.41
1	Berlin	Treptow, Treptower Park	Urban	-	1998	52 2917.71	13 288.60
1	Berlin	Wedding Ploetzensee	Urban	-	1935	52 3232.96	13 1950.27

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
6	Berlin	Weissensee	Urban	-	1913; 1918; 1927; 1943; 1944	52 3311.25	13 2732.00
6	Berlin	Weissensee, Falkenbergstrasse	Urban	Urban	1971	52 3320.42	13 2835.93
3	Berlin	Wilmersdorf	Urban	-	1905	52 2933.70	13 1923.85
2	Berlin	Wuhlheide	Urban	-	1935; 1936	52 2743.86	13 3213.03
1	Berlin	Zehlendorf	Urban	-	1913	52 2716.40	13 405.74
2	Berlin	Treptow-Koepenick, Krummendammer Heide	Urban	-	2017	52 46.215	13 63.198
2	Berlin	Charlottenburg-Wilmersdorf, Heerstrasse	Urban	Urban	2017	52 50.828	13 25.248
2	Berlin	Tempelhof-Schoeneberg, Park am Gleisbereich, Flaschenhalspark	Urban	Urban	2017	52 48.854	13 37.276
2	Berlin	Steglitz-Zehlendorf, Dueppeler Forst, Schloss Glienicke	Urban	-	2017	52 2446.01	13 547.29
2	Berlin	Steglitz-Zehlendorf, Glienicker Volkspark	Urban	Urban	2017	52 41.562	13 09.988

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
3	Berlin	Charlottenburg-Wilmersdorf, Grunewald, Am Postfenn	Urban	-	2017	52 50.058	13 22.444
2	Berlin	Mitte, Tiergarten	Urban	Urban	2017	52 51.451	13 37.353
7	Berlin	Berlin-Mitte, Tiergarten	Urban	Urban	2017	52 51.426	13 37.576
1	Berlin	Pankow, Blankenfelde	Urban	-	2017	52 63.390	13 39.376
2	Berlin	Spandau, Gatow	Urban	-	2017	52 47.737	13 12.965
4	Berlin	Pankow, Kladow	Urban	-	2017	52 61.662	13 44.811
9	Berlin	Tempelhof-Schoeneberg, Tempelhofer Feld	Urban	-	2017	52 47.541	13 40.603
1	Berlin	Neukoelln, Fritz-Erler-Allee	Urban	Urban	2017	52 43.653	13 45.144
1	Berlin	Treptow-Koepenick, Stubenrauchstrasse	Urban	Urban	2017	52 43.429	13 49.902
1	Brandenburg	Ahrensfelde	Rural	-	1970	52 3454.19	13 3429.25
1	Brandenburg	Arkenberge, Natural reserve	Rural	Near natural	1981	52 3841.75	13 253.56

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
1	Brandenburg	Barnim	Rural	-	1983	52 5126.80	13 4159.39
2	Brandenburg	Barnim, Werbellinsee	Rural	-	1983	52 5526.4	13 4347.47
1	Brandenburg	Basdorf	Rural	-	1971	52 438.92	13 265.73
1	Brandenburg	Bernau	Rural	-	1919	52 4126.48	13 3425.04
9	Brandenburg	Blumberg	Rural	-	1970; 1975; 1988	52 3615.08	13 3741.00
9	Brandenburg	Brandenburg an der Havel	Rural	-	1967; 1970	52 2314.12	12 327.61
14	Brandenburg	Brandenburg an der Havel, Rietzer See, Natural reserve	Rural	Near natural	1978; 1979	52 2239.59	12 3837.63
1	Brandenburg	Bredow	Rural	-	1930	52 359.42	12 5544.16
5	Brandenburg	Brieselang	Rural	-	1921; 1923; 1924; 1927	52 344792	12 5859.21
1	Brandenburg	Brieselang, Bredower Forst	Rural	-	1941	52 3423.84	13 22.33
1	Brandenburg	Buhnenwerder, Protected landscape	Rural	Near natural	1979	52 2328.48	12 2937.86

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
1	Brandenburg	Chorin	Rural	-	1949	52 5428.74	13 5228.72
1	Brandenburg	Cottbus, Hoyerswerda, Inland dunes	Rural	-	1987	51 278.20	14 1624.21
2	Brandenburg	Dueberitz	Rural	-	1923; 1924	52 3212.05	13 224.07
2	Brandenburg	Eberswalde	Rural	-	1966	52 4938.67	13 5142.25
1	Brandenburg	Egsdorf, Teupitzer See	Rural	-	1970	52 815.92	13 3718.10
1	Brandenburg	Eisenhuettenstadt	Rural	-	1980	52 729.95	14 3826.17
6	Brandenburg	Erkner	Rural	-	1983	52 256.98	13 4450.84
8	Brandenburg	Finkenkrug	Rural	-	1909; 1910; 1943	52 3314.76	13 237.68
11	Brandenburg	Fürstenwalde, Wernsdorfer See, Protected landscape	Rural	Near natural	1978; 1980; 1981; 1986	52 2250.96	13 4346.21
1	Brandenburg	Gosen, Neu-Zittau, Wernsdorfer See, Protected landscape	Rural	Near natural	1985	52 2343.35	13 4334.08
1	Brandenburg	Groß Machnow	Rural	-	1983	52 1620.82	13 279.98

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
1	Brandenburg	Groß Schönebeck, Schorfheide, Wildlife park	Rural	-	1932	52 549.39	13 3116.15
3	Brandenburg	Großkoschen	Rural	-	1985	51 2919.30	14 224.59
2	Brandenburg	Gruenheide	Rural	-	1970; 1980	52 250.92	13 486.53
1	Brandenburg	Grunow, Dammdorf	Rural	-	1906	52 831.43	14 2452.29
2	Brandenburg	Henningsdorf	Rural	-	1975	52 3735.49	13 1031.97
6	Brandenburg	Herzfelde	Rural	-	1931; 1943	52 2825.84	13 5124.52
1	Brandenburg	Hohen Neuendorf	Rural	-	1973	52 3953.12	13 168.97
1	Brandenburg	Hohen Neuendorf, Borgsdorf	Rural	-	1913	52 4245.54	13 1610.60
1	Brandenburg	Holzberg, Rietser See, Natural reserve	Rural	Near natural	1977	52 230.23	12 3856.73
3	Brandenburg	Hoenow	Rural	-	1923; 1928; 1930	52 3242.79	13 3823.38
2	Brandenburg	Hoenow, Mehrow	Rural	-	1939; 1978	52 3422.27	13 3818.36
2	Brandenburg	Hoppegarten	Rural	-	1980	52 3040.26	13 4018.39

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
2	Brandenburg	Juehnsdorf	Rural	-	1947	52 185.28	13 230.63
1	Brandenburg	Kablow	Rural	-	1975	52 2734.30	13 815.30
1	Brandenburg	Klein-Mutz	Rural	-	1980	52 5715.96	13 177.84
8	Brandenburg	Lebus an der Oder	Rural	-	1935; 1971; 1979; 1986	52 250.37	14 3154.98
1	Brandenburg	Lebus an der Oder, Oderbruch	Rural	-	1981	52 2530.86	14 3042.28
3	Brandenburg	Lebus an der Oder, Priesterschlucht	Rural	-	1975	52 2841.57	14 3227.08
1	Brandenburg	Lotschesee	Rural	-	1968	52 4847.65	13 3014.64
1	Brandenburg	Luckau	Rural	-	1970	51 5110.94	13 4235.91
6	Brandenburg	Ludwigsfelde, Wietstock	Rural	-	1942	52 184.12	13 1541.86
1	Brandenburg	Machnow	Rural	-	1932	52 1615.57	13 2736.26
1	Brandenburg	Mahlow, Blankenfelde	Rural	-	1947	52 2053.13	13 2412.99

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
8	Brandenburg	Mallnow	Rural	-	1979; 1982; 1986; 1993; 1994	52 2149.88	13 2312.81
17	Brandenburg	Mallnow, Natural reserve	Rural	Near natural	1975	52 192.66	13 2112.69
1	Brandenburg	Mildenberg	Rural	-	1998	53 028.37	13 1745.98
2	Brandenburg	Mittenwalde	Rural	-	1983	52 1548.21	13 323.78
9	Brandenburg	Muehlenbeck	Rural	-	1949; 1973; 1974	52 3959.32	13 2249.22
7	Brandenburg	Muencheberg	Rural	-	1980	52 3024.90	14 741.38
3	Brandenburg	Nauen	Rural	-	1910; 1927; 1942	52 3624.90	12 5253.36
2	Brandenburg	Nauen, Nauener Stadtforst	Rural	-	1921	52 3822.79	12 5724.98
1	Brandenburg	Neuendorf	Rural	-	1982	51 369.14	11 538.83
3	Brandenburg	Oderberg, Gravel surface	Rural	-	1990	52 528.15	14 210.65
2	Brandenburg	Potsdam, Ferch	Rural	-	1973	52 1819.35	12 555.83

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
7	Brandenburg	Potsdam, Großbeeren	Rural	-	1982	52 2133.91	13 1832.17
13	Brandenburg	Potsdam, Surroundings	Rural	-	1977; 1978; 1979	52 210.45	13 85.14
1	Brandenburg	Rathenow	Rural	-	1969	52 3457.31	12 1911.15
14	Brandenburg	Ruedersdorf	Rural	-	1899; 1943; 1969; 1994	52 2853.73	13 5014.62
2	Brandenburg	Schiffmuehle	Rural	-	1990	52 4819.57	14 526.26
1	Brandenburg	Schildow	Rural	-	1974	52 400.11	13 2212.35
1	Brandenburg	Schildow, Arkenberge, Natural reserve	Rural	Near natural	1981	52 3835.99	13 256.13
2	Brandenburg	Schildow, Moenchmuehle	Rural	-	1972	52 3848.96	13 2254.16
7	Brandenburg	Schildow, Natural reserve	Rural	Near natural	1981	52 3824.74	13 210.35
1	Brandenburg	Schmerzke	Rural	-	1971	52 239.59	12 3537.60
1	Brandenburg	Schoenborn	Rural	-	1933	51 3556.63	13 2917.07

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
17	Brandenburg	Schoenfließ	Rural	-	1967; 1972; 1973; 1977; 1981; 1985	52 3912.96	13 2025.65
12	Brandenburg	Sperenberg	Rural	-	1930; 1937; 1082	52 815.92	13 2155.28
9	Brandenburg	Strausberg	Rural	-	1893; 1934; 1946; 1965; 1983; 1987	52 3352.28	13 5240.52
1	Brandenburg	Telz	Rural	-	1934	52 1449.39	13 2846.78
1	Brandenburg	Tiefensee	Rural	-	1932	52 410.63	13 5018.53
1	Brandenburg	Toepchin	Rural	-	1991	52 101928	13 343797
10	Brandenburg	Wandlitz	Rural	-	1972; 1973	52 4515.19	13 2821.97
2	Brandenburg	Wernsdorf	Rural	-	1974	52 231.95	13 4223.01
1	Brandenburg	Wernsdorf, Wernsdofer See, Protected landscape	Rural	Near natural	1974	52 2046.36	13 412.45
3	Brandenburg	Wietstock	Rural	-	1942	52 164.82	13 1833.95
7	Brandenburg	Wildau	Rural	-	1942; 1943	52 1933.38	13 3734.44

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
1	Brandenburg	Zossen	Rural	-	1991	52 131.11	13 2713.65
1	Brandenburg	Zossen, Hostfelde	Rural	-	1991	52 1241.79	13 2427.57
26	Brandenburg	Nordwestuckermark	Rural	Agricultural landscape (Winter wheat, Separating green spaces)	2016	53 2221.15	13 404.43
11	Brandenburg	Falkenhagen	Rural	Agricultural landscape (Winter wheat, Separating green spaces)	2017	53 20.746	13 44.327
20	Brandenburg	Arendsee	Rural	Agricultural landscape (Winter wheat, Separating green spaces)	2017	53 20.334	13 39.330
7	Brandenburg	Guestow	Rural	Agricultural landscape (Winter wheat, Separating green spaces)	2017	53 20.611	13 45.943
4	Brandenburg	Fuerstenwerder	Rural	Agricultural landscape (Winter wheat, Separating green spaces)	2017	53 23.302	13 35.736

Number of individuals	Area	District	Region	Habitat	Time	GPS coordinates	
						Latitude	Longitude
1	Brandenburg	Strausberg	Rural	Agricultural landscape (Winter wheat, Soy, Separating green spaces)	2017	52 33 41.77-35.51	13 54.20.56-27.69
2	Brandenburg	Brandenburg, Blankenfelde-Mahlow	Rural	Agricultural landscape (Winter wheat, Soy, Separating green spaces)	2017	52 33.962	13 38.178
1	Brandenburg	Brandenburg, Blankenfelde-Mahlow	Rural	Agricultural landscape (Winter wheat, Soy, Separating green spaces)	2017	52 33.882	13 38.759

7 Declaration of independence / Eigenständigkeitserklärung

Hereby I certify that I have written the present work independently and have used no other than the specified tools. The parts of the work taken from other works, either verbally or in terms of content, have been identified by corresponding information from the sources. The underlying doctorate regulations are known to me, the work corresponds to the principles of the Humboldt University in Berlin to ensure good scientific practice. This work did not exist in the same or similar form to any examining authority.

Hiermit versichere ich, dass ich die vorliegende Arbeit selbstständig verfasst und keine anderen als die angegebenen Hilfsmittel benutzt habe. Die Stellen der Arbeit, die anderen Werken wörtlich oder inhaltlich entnommen sind, wurden durch entsprechende Angaben der Quellen kenntlich gemacht. Die zugrunde liegende Promotionsordnung ist mir bekannt, die Arbeit entspricht den Grundsätzen der Humboldt-Universität zu Berlin zur Sicherung guter wissenschaftlicher Praxis. Diese Arbeit hat in gleicher oder ähnlicher Form noch keiner Prüfungsbehörde vorgelegen.

Silvia Keinath, Berlin, den 24 Juni 2021